POPULATION ECOLOGY OF WILLOW PTARMIGAN (*LAGOPUS LAGOPUS*) IN THE PRESENCE OF SPATIALLY CONCENTRATED HARVEST

By

Graham G. Frye

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APPROVED:

Dr. Mark Lindberg, Committee Chair
Dr. Scott Brainerd, Committee Member
Dr. Knut Kielland, Committee Member
Dr. Joshua Schmidt, Committee Member
Dr. Knut Kielland, Chair
Wildlife Biology and Conservation Program
Dr. Kinchel Doerner, Dean
College of Natural Science and Mathematics
Dr. Michael Castellini, *Dean of the Graduate School*

Abstract

Understanding the potential effects of harvest on wildlife populations is fundamental to both theoretical wildlife science and applied wildlife management. The effects of harvest on wildlife populations vary dramatically and depend on the timing and magnitude of harvest, as well as population-specific states and vital rates. Demographic compensation plays a key role in models of wildlife population dynamics and in developing harvest strategies. However, the degree and form of compensation in a given population depends on its particular ecological and life history characteristics, resulting in the need for population-specific assessments of responses to harvest.

Ptarmigan (*Lagopus* spp.) are ecologically important species and are culturally valued for subsistence and recreational hunting throughout the Holarctic. In Alaska, willow ptarmigan (*L. lagopus*) are among the most commonly harvested small game species, but the population-level effects of harvest are not well understood. Investigating the population-level effects of harvest on these populations would aid harvest management and increase general understanding of the ecology of the species. To this end, I studied the population ecology of willow ptarmigan in a region of Alaska with spatially concentrated harvest along access corridors. I investigated: (1) the effect of harvest, season, and demographic group on survival, (2) the effect of harvest on breeding densities, (3) dispersal and seasonal movements patterns in relation to harvest, and (4) temporal and observer effects on ptarmigan survey efforts. I found that survival rates and breeding densities of willow ptarmigan in heavily hunted areas were substantially lower than those in remote sites without hunting. We did not observe seasonal compensatory mortality and the potential for permanent immigration (i.e., breeding/natal dispersal) to compensate for harvest appeared limited. However, seasonal movements away from breeding territories appeared to distribute the effects of harvest more evenly among ptarmigan from accessible and remote areas during winter and early spring. This suggests that the timing of hunting seasons may play a critical role in deter-

mining effects on ptarmigan densities in accessible breeding areas, with early autumn (prior to initiation of seasonal movements) harvest likely having the greatest impact. In addition, when examining ptarmigan survey methodology, I found substantial temporal heterogeneity in the availability of ptarmigan for detection during surveys, as well as variation in observer-specific detection rates. This underscores the importance of investigators considering the role of imperfect and heterogeneous detection when designing ptarmigan monitoring strategies to avoid inaccurate conclusions about abundance and trends.

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Chapter 1: General Introduction

Consequences of the consumptive use of wildlife are a central focus of ecological research in the modern world (Williams et al. 2001). In order to understand the way in which harvest affects wildlife populations, it is necessary to examine how it influences population states (e.g., density, abundance) and vital rates (e.g., survival, reproduction). Understanding how harvest alters these population characteristics is essential to the conservation of populations and to ensuring that harvest can be sustained in perpetuity.

Ptarmigan (*Lagopus* spp.) are ecologically important species and are culturally valued for subsistence and recreational hunting throughout the Holarctic (Hannon et al. 1998). In Alaska, willow ptarmigan (*L. lagopus*) are among the most commonly harvested small game species (Merizon et al. 2015), but the population-level effects of this harvest are not well understood. Moreover, hunting in Alaska occurs largely along a limited number of access corridors, which results in spatially concentrated harvest in accessible areas. This underscores the need for research on the population ecology of Alaskan ptarmigan populations in relation to harvest. In this dissertation, I examine the effects of harvest on willow ptarmigan population dynamics, as well as elucidate aspects of ptarmigan ecology and survey methodology in subarctic Alaska.

In Chapter 2 of this dissertation, I compare the seasonal survival rates of willow ptarmigan from sites along access corridors that receive heavy use from ptarmigan hunters to those from remote sites that receive minimal human use. I deployed radio-transmitters on willow ptarmigan during the breeding season, located those individuals monthly to determine survival status, and used those data to estimate seasonal and annual survival rates for adult males, adult females, and juveniles. In addition, we used matrix projection models to assess the viability of accessible and remote populations in the absence of immigration. Our results provide insight into compensatory processes and have implications for the sustainability of ptarmigan harvest in heavily used access corridors.

In Chapter 3, I compare the breeding densities of willow ptarmigan at the accessible and remote sites. I used a distance sampling approach to estimate the number of breeding territories at sites of each type. Estimating breeding densities provides an important link to the vital rate comparisons of Chapter 2 and bolsters our conclusions about the role of compensatory processes in these populations.

In Chapter 4, I further develop our understanding of the population dynamics of willow ptarmigan relative to harvest by examining the movement ecology of willow ptarmigan in our study area. I used radio-transmitters to locate individual ptarmigan monthly and recorded locations. This elucidates both permanent immigration processes (breeding and natal dispersal) and temporary seasonal movement patterns. The timing and magnitude of these movements, coupled with the vital rate and density estimates from Chapters 2 and 3, provide a picture of the dynamics that shape population responses in areas with concentrated ptarmigan harvest.

In Chapter 5, I describe a methodological study on factors that influence the detection process during ptarmigan surveys. I conducted repeat-visit point count surveys and modeled temporal effects on the availability of ptarmigan for detection and observer-specific effects on the detectability of available ptarmigan. I then simulated surveys based on these estimates to assess the influence of detection heterogeneity on trend estimation. The results provide insight into the detection process and have direct implications for designing reliable ptarmigan surveys.

The chapters of this dissertation together provide a novel picture of the population dynamics of ptarmigan in the presence of concentrated consumptive use by humans relative to populations exposed to little or no hunting. In addition, I provide insight into factors that influence the reliability of population surveys and that therefore have implications for identifying appropriate ptarmigan harvest management strategies.

1.1 References

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Chapter 2: Willow Ptarmigan Survival and Population Stability in Areas with Concentrated Harvest and Adjacent Refugia[1]

2.1 Abstract

The effects of hunting on wildlife populations vary dramatically and depend on the timing and magnitude of harvest, as well as population-specific states and vital rates. We examined the hypothesis that spatially and seasonally concentrated harvest decreases annual survival probabilities of willow ptarmigan because of a lack of seasonal compensatory mortality. We estimated survival of radio-marked willow ptarmigan (*Lagopus lagopus*) at sites that were easily accessible and heavily hunted, in addition to sites that were remote and received little or no hunting pressure in Alaska, USA. We predicted that seasonal survival estimates during the ptarmigan hunting season would be lower in access corridors than at remote sites and that this would result in lower annual survival because of the absence of complete seasonal compensatory mortality. Consistent with our prediction, annual survival estimates at remote sites were higher than those at accessible sites, as were monthly estimates during most seasons. At remote sites, annual survival of adult males (0.50, 95% CrI: 0.42-0.57) was higher than that of adult females (0.36, 95% CrI: 0.25-0.46) and juveniles (0.35, 95% CrI: 0.24-0.45). At accessible sites annual survival was likewise higher for males (0.36, 95% CrI: 0.26-0.46) than for adult females (0.22, 95% CrI: 0.12-0.32) and juveniles (0.24, 95% CrI: 0.11-0.36). During the nesting, brood-rearing, and autumn dispersal seasons, survival was higher at remote sites than accessible sites when accounting for demographic group (adult male, adult female, juvenile), whereas survival did not differ between sites during the winter and pre-breeding seasons. During the winter and pre-breeding seasons, seasonal movements resulted in the spatial redistribution of ptarmigan, such that they were no longer spatially segregated by accessibility of their breeding/natal sites. The pattern of differential mortality during seasons in which ptarmigan were clearly delineated into remote and accessible sites,

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coupled with nearly identical survival rates during the seasons in which they were not, suggested a possible additive component of harvest mortality on ptarmigan survival.

In addition, we assessed the potential impact of harvest-induced spatial heterogeneity in survival on local population stability using matrix population models fit with estimated vital rates. Hypothetical projections, assuming geographic closure, suggested that the survival rate at accessible sites was low enough to make accessible ptarmigan populations unsustainable without net immigration ($\hat{\lambda} = 0.71$ [95% CrI: 0.44–0.96]). In contrast, survival rates at remote sites were probably high enough to allow some population growth and/or emigration ($\hat{\lambda} = 1.05$ [95% CrI: 0.82–1.28]).

2.2 Introduction

Fundamental to the study of population ecology is an understanding of the vital rates that govern population dynamics. Although monitoring population states can provide useful information to researchers and managers, a focus on population states alone can be misleading (Fretwell and Lucas 1969, Van Horne 1983). A comprehensive understanding of the mechanisms underlying population states requires the estimation of vital rates and identification of the factors that influence them.

Survival is a key vital rate, which can be influenced by myriad spatially, temporally, and demographically variable factors. Spatial variation in survival can arise from a variety of causes, including habitat quality (Van Horne 1983), population density (Lack 1954, Hanski 2001), predation, and harvest (Sandercock et al. 2011). Temporal survival dynamics can be driven by variation in exposure to both top-down and bottom-up forces, which are often associated with seasonal aspects of life history and behavior (Ricklefs 1992, Sherry and Holmes 1995, Sillett and Holmes 2002). Demographic variation in vital rates can have profound implications for population dynamics. For example, in monogamous birds, females typically exhibit lower survival rates than males (Trivers 1985, Lack 1968, Promislow et al. 1992, Liker and Szkely 2005). This means that the sex that exhibits lower survival rates is

the same sex that produces young, which limits subsequent recruitment of juveniles into the breeding population.

For exploited species, the magnitude, timing, and demographic focus of exploitation also has the potential to influence population dynamics. In particular, excessive or ill-timed harvest can result in additive mortality or decreased recruitment (Burnham and Anderson 1984, Pollock et al. 1989, Roland et al. 2010, Blomberg 2015, Caudill et al. 2017). In addition, differential harvest of individuals that exhibit heterogeneity in reproduction or survival has implications for the effect of harvest at the population level (Johnson 1984, Lebreton 2005, Lindberg et al. 2013, Caudill et al. 2017), These factors can ultimately impact the stability of populations, as well as opportunities for sustainable future harvest.

Ptarmigan (*Lagopus* spp.) are ecologically important species throughout their circumpolar ranges. They are key prey species for a variety of avian and mammalian predators and are thought to play an important role in the numerical cycles typical of many arctic and boreal vertebrates (Boutin et al. 1995). Moreover, they are culturally valued species for subsistence and recreational hunting in both North America and Eurasia. As such, an understanding of the relationship between harvest, survival rates, and population dynamics is essential for effective management of ptarmigan populations.

Willow ptarmigan (*Lagopus lagopus*) are among the most popular small game species in much of boreal and arctic North America. In Alaska, USA, ptarmigan compose approximately 54% of the statewide annual upland game bird harvest, with willow ptarmigan accounting for the majority of the ptarmigan harvest (Merizon et al. 2015). However, the magnitude of willow ptarmigan harvest varies dramatically among regions in Alaska, largely because of limited access to most areas of the state. This has resulted in an association between heavy harvest and road-access corridors. Unfortunately, detailed information on the impact and sustainability of concentrated ptarmigan hunting within access corridors is limited; however, recent estimates suggested low breeding densities of willow ptarmigan in these corridors (Chapter 3).

Our goal was to estimate the spatial, temporal, and demographic variation in survival of willow ptarmigan in a region of Alaska exposed to concentrated harvest along access corridors and limited hunting in adjacent areas. In addition, we examined the hypothesis that seasonally concentrated harvest decreases annual survival probabilities of willow ptarmigan and used estimated survival and reproductive rates to assess the potential impact of harvest induced spatial heterogeneity in survival on local population stability. We predicted that seasonal survival estimates during the ptarmigan hunting season would be lower in access corridors than at remote sites, and that annual survival estimates would be lower in access corridors in the absence of seasonal compensation in mortality.

2.3 Study Area

We conducted this study in the southern Alaska Range and northern Talkeetna Mountains in southern Interior Alaska, USA (Figure 2.1). Within this region, we designated five study sites, which differed in their degrees of accessibility. We categorized the Denali Highway and Butte Lake sites as accessible (highway vehicle access), and the Big Lake, Fog Creek, and Busch Creek sites as remote (access primarily by small aircraft). Sites were similar in terms of habitat characteristics, but differed in the degree of use for hunting and other recreational activities. Use of the accessible study sites was substantial and included ptarmigan hunting, as well as non-hunting recreation (e.g., hiking, all-terrain vehicle use, snowmobile use). In contrast, human use of the remote sites was limited. Elevations at the study sites ranged from 850 to 1,230 m. These sites contained a mix of barren rocky slopes, open tundra-dominated hills, shrub tundra, and riparian areas. Shrub species were primarily dwarf birch (*Betula nana*, *B. glandulosa*), alder (*Alnus* spp.), and willow (*Salix* spp.). Lower elevations were characterized by subalpine spruce (*Picea* spp.) stands and taller stands of dwarf birch. The hunting season for willow ptarmigan on the study area ran from 10 Aug–31 March, with a bag limit of 10 ptarmigan per day.

2.4 Methods

2.4.1 Field Methods

We deployed VHF radio-transmitters on ptarmigan from 2013-2015. We captured adults (10 months old) during April, May, and August, and we captured juveniles ($\backsim$60–80 days old) during August. We located territorial ptarmigan using a combination of visual scanning and eliciting vocal responses with broadcasted recordings of conspecific vocalizations. After locating ptarmigan, we lured individuals into the vicinity of capture equipment using conspecific decoys and recordings of conspecific vocalizations. We captured ptarmigan using: (1) mist nets erected in flight lanes, (2) gill nets strung around vegetation, through which ptarmigan travelled on foot, (3) hand-held net guns to capture birds in flight, perched, or walking, (4) noose carpets constructed with monofilament snares to capture birds that approached decoys closely, and (5) bow nets to capture birds that approached decoys closely. Upon capture, ptarmigan were fitted with 12 g VHF transmitters (Advanced Telemetry Systems, Isanti, MN, USA), using necklace-style harnesses (Amstrup 1980). Transmitters weighed $< 3\%$ of body weight for all radio-marked individuals. Each transmitter contained a mortality switch that increased the pulse rate of VHF signals after 10 hrs of inactivity.

We located radio-marked ptarmigan approximately monthly from June 2013 through June 2016 using small fixed-wing aircraft. During aerial telemetry flights, we recorded the location of radio-marked birds using Global Positioning System (GPS) receivers and the status of the mortality switch on each transmitter. If a transmitter was on mortality mode, we located it again during at least one subsequent flight or visited the site on the ground to ensure that the mortality signal was accurate. Because of the remote and diffuse distribution of ptarmigan on our study area, we did not attempt to evaluate cause of death for all mortality events. Between 01 August and 28 August, we visually located as many surviving radio-marked birds as possible on the ground at our study sites and estimated the number of juveniles associated with each radio-marked adult. At least two observers approached radio-

marked adults closely from different angles to count juveniles. When vegetation obscured the view of broods or provided locations for juveniles to hide, we used drag ropes and walked a grid pattern centered on the radio-marked adult in an effort to stimulate movement of hidden juveniles. We revisited each previously visited adult at least once to re-count associated juveniles or ensure that no brood was present. If counts differed between visits to an individual adult, then the maximum number counted was used as the estimate of brood size. Brood counts occurred at all sites except the Busch Creek site.

2.4.2 Data Analysis

We used discrete-time, binomial survival models (Pollock et al. 1989, White and Garrot 1990, Dinsmore et al. 2002, Schmidt et al. 2010) to model spatial, temporal, and demographic variation in the survival process. Season was the temporal covariate considered in the model. We estimated monthly survival probabilities for five seasons such that they depicted biologically distinct periods of the year (Table 2.1). Seasons were delineated on the basis of local observations of the breeding and migration phenology of willow ptarmigan. Additionally, we included a binary spatial covariate representing the accessibility of each individuals breeding or natal site. This spatial term was binary with one level representing ptarmigan captured at the accessible sites, which were relatively easy to access from the Denali Highway (0–7 km distant from the highway) and thus received substantial use by hunters (both on foot and on mechanized transport, such as ATVs and snowmobiles). In contrast, the remote sites were more difficult to access (34-80 km from the highway and accessible primarily via small plane or helicopter) and received little or no use by hunters. We also specified an age-sex covariate with three levels: adult male, adult female, and juvenile. Juveniles were considered a single group because of the difficulty in discerning sex based on morphology during the first months of life (Pyle 2008).

We used a logit link function to model the probability that individual i survived from time t-1 to time t as a function of a linear combination of covariates:

$$Y_{i,t}|Y_{i,t-1} \backsim \text{Bernoulli}(Y_{i,t-1}\phi_{i,t}^{t})$$

$$\text{logit}(\phi_{i,t}^{t}) = \boldsymbol{x}_{\boldsymbol{i,t}}'\boldsymbol{\beta} + \boldsymbol{z_i}$$

$$\boldsymbol{z_i} \backsim \text{Gaussian}(0, \sigma^2)$$

where $Y_{i,t}$ is the survival state of individual i at time t, $\phi_{i,t}$ is the probability of individual i surviving from time t-1 to time t, $x_{i,t}$ is a vector of covariate values for individual i during the interval preceding time t, β is the corresponding vector of coefficients, and z_i is an individual-specific Gaussian distributed random intercept. In the logit transformation, $\phi_{i,t}$ was raised to the power of t to account for variation in exposure period between telemetry locations (Shaffer 2004). We assumed that censoring (e.g., transmitter-failure, failure to locate a signal during telemetry flights) was independent of the survival process. We first fit a base model with main effects of age/sex, site, and season, as well as an interaction between site and season to allow flexibility in the estimated effect of site across seasons. We then fit additional models by adding all other possible two- and three-way interactions between these covariates to allow temporal and spatial survival patterns to differ among demographic groups in a non-additive manner. This resulted in fitting five total models. Inference was based on the model structure that yielded the lowest value of the Leave-One-Out Information Criterion (LOOIC, Vehtari et al. 2017), which is an approximation of the out-of-sample prediction accuracy estimate obtained using cross validation (Stone 1977), and is similar to the Watanabe Information Criterion (Watanabe 2013). The LOOIC computations were implemented in the R software environment (R Core Team 2017), using the package loo (Vehtari et al. 2016)

We implemented models in a Bayesian framework and gave all parameters vague priors to minimize the role of prior specifications in posterior inference. We gave parameters in β Uniform(-5,5) priors on the logit scale. To fit the model, we used a Markov Chain Monte Carlo (MCMC) algorithm with four chains in JAGS (Plummer 2017). We used 20,000 sam-

ples from the joint posterior, plus 1000 burn-in and 1000 adaptation samples. We assessed convergence using trace plots and R-hat statistics (Gelman and Rubin 1992).

We derived posterior distributions for annual survival as the product of seasonal survival parameters and derived annual survival parameters for each age/sex class at remote and accessible sites (i.e., six derived quantities). We also derived posterior distributions for the difference between parameters to compare parameter estimates of interest,. The proportion of each of these derived posterior distributions that was greater than zero represented the probability that one parameter was greater than the other. Rather than choose a fixed threshold at which to infer a difference (e.g., via fixed alpha levels or credible interval levels for the differences), we present the probability that one parameter is greater than another, along with 95% credible intervals (CrI) for each individual parameter.

To assess the potential population-level implications of estimated spatial variation in survival rates we parameterized simple female-based age-structured matrix projection models (Caswell 2001) separately for remote and accessible sites. We assumed birth-pulse reproduction, a post-breeding census at the end of the nesting season, and a transition to the adult age class upon entering the first nesting season (i.e., May of the second year of life). We constructed the projection matrices with parameters representing fertility and survival for each age class:

$$\begin{bmatrix} F_a & F_j \\ S_a & S_j \end{bmatrix}$$

where F_j represents the juvenile fertility rate and is fixed at 0, F_a represents the adult fertility rate which is the product of per capita production (i.e., number of chicks per female) and the proportion of the juvenile population that is female. We assumed a 1:1 sex ratio for juveniles. S_j is the probability of survival from the juvenile to adult age class, and S_a is the probability that adults survive to the subsequent birth pulse. We used estimates

of annual survival probability and reproductive output from this study to fit the models, while treating each population as geographically closed (i.e., no immigration or emigration). Geographic closure was not a realistic assumption, but this enabled us to assess the potential importance of immigration to local population stability. To estimate the finite rate of increase (λ) for each scenario, we computed the dominant eigenvalue for the associated projection matrix, assuming a stable age distribution. To depict the uncertainty in estimates of λ, we used Monte Carlo simulation to sample from the posterior density of each annual survival parameter in the matrix model. We fixed the production component of the adult fertility parameter (brood size in August) at the mean value across all study sites and used 100,000 iterations of the Monte Carlo algorithm.

2.5 Results

We deployed necklace-mounted VHF radio-transmitters on 243 willow ptarmigan between April 2013 and August 2015. The radio-marked sample was composed of 113 adult males, 62 adult females, and 68 juveniles. We based inference on the base model, which contained additive terms for sex, site, and season and a two-way interaction between site and season. This model yielded a LOOIC value of 1041.9, which was 5.1-17.9 LOOIC units lower than the other covariate-interaction structures considered.

2.5.1 Demographic Variation in Survival

When accounting for site-type (i.e., accessible vs. remote), adult males exhibited the highest seasonal survival probabilities followed by adult females, and then juveniles (Figure 2.2). Correspondingly, annual survival was higher for adult males (accessible: 0.36 [95% CrI: 0.26-0.46]; remote: 0.50 [95% CrI: 0.42-0.57]) than for adult females (accessible: 0.22 [95% CrI: 0.12-0.32]; remote: 0.36 [95% CrI: 0.25-0.46]) or juveniles (accessible: 0.24, 95% CrI: 0.11-0.36]; remote: 0.35 [95% CrI: 0.24-0.45]), when accounting for site-type (Figure 2.3). Annual survival was similar for adult females and juveniles; however, the annual survival

period for juveniles encompassed only four seasons (brood rearing through pre-breeding) because juveniles enter the sample during the brood-rearing period of their natal year and we defined the transition to adulthood as occurring in the nesting season of their second year of life.

2.5.2 Spatial and Temporal Variation in Survival

Survival estimates were lower at accessible sites than remote sites for all age/sex classes during nesting, brood-rearing, and fall movement seasons (Figures 2.2 and 2.6). Derived probability densities for seasonal differences suggested that survival was higher at remote sites during these seasons with probabilities of 94.5%, 98.3%, and 94.3%, respectively. In contrast, survival estimates were similar between remote and accessible sites for all age/sex classes during the winter and spring seasons (Figures 2.2 and 2.6). The derived probabilities that survival was lower at accessible sites during these seasons were 51.1% and 45.0%, respectively. Differences in these seasonal estimates corresponded with the seasonal movements of ptarmigan. During nesting, brood-rearing, and fall movement seasons, ptarmigan were segregated into remote and accessible sites, whereas seasonal movements away from breeding territories resulted in the spatial mixing of ptarmigan from remote and accessible sites during the winter and spring seasons. As with seasonal differences, annual survival was higher at remote sites than accessible sites for all age/sex classes (Figures 2.3 and 2.5). The probability that annual survival was higher at remote sites was 98.4% for both adult males and adult females, and 93.7% for juveniles.

2.5.3 Local Population Stability

Projections for lambda suggested that—in the absence of immigration/emigration—remote populations would most likely be stable or slightly increasing, whereas accessible populations would probably decrease (Figure 2.4). Based on our brood count data, the estimated mean number of chicks per brood was 3.8 (SE = 0.4, n = 62). Conditional on the

estimated vital rates, there was a 63.2% probability (odds ratio = 2.9) that remote populations would increase ($\lambda > 1$) and a 96.0% probability (odds ratio = 576.0) that accessible populations would decrease ($\lambda < 1$).

2.6 Discussion

Estimates of spatial, temporal, and demographic variation in survival were consistent with our hypothesis that seasonally concentrated harvest decreases annual survival probabilities for willow ptarmigan. Differences in seasonal survival estimates resulted in lower annual survival in access corridors than in remote sites, owing to a lack of seasonal compensation in mortality. The pronounced disparity in projected population growth rates suggested that ptarmigan populations in the accessible areas would decrease dramatically in the absence of immigration from adjacent refugia.

2.6.1 Demographic Variation in Survival

Consistent with theory, we found that annual survival of females was lower than that of males (Figure 2.3). Relatively few sex-specific willow ptarmigan survival estimates are available for comparison with previous studies. Bergerud (1970) indicated that annual survival of female willow ptarmigan was lower than that of males in Newfoundland, Canada, whereas Smith and Willebrand (1999) did not detect differences in survival rates between males and females in Sweden. Sandercock et al. (2005) estimated annual survival of female willow ptarmigan to range from 0.33 to 0.43 in two populations exposed to low harvest pressure. Similarly, Hannon et al. (2003) estimated a range of annual survival probabilities of 0.30–0.54 for females during an eight-year period in a population exposed to some harvest in northern British Columbia, Canada. Our estimates are consistent with these past studies. Annual survival estimates for male willow ptarmigan in previous studies (0.29–0.67, Pedersen 1984; 0.43–0.63, Hannon et al. 2003) were also similar to those at remote sites in our study (0.50). Alaskan rock ptarmigan exhibit similar demographic patterns in mortality (*Lagopus*

muta; Merizon et al. 2018).

There are several potential reasons for sex-specific differences in annual survival of willow ptarmigan. In some species, greater female parental investment may explain differential survival (Williams 1966, Trivers 1972, Owens and Bennet 1994); however, willow ptarmigan are atypical tetraonids in that they exhibit biparental care throughout the period of juvenile dependence (Weeden 1963, Wittenberger 1978). Thus, male willow ptarmigan are exposed to greater risk during this period than males of other tetraonid species. The possible exception to this occurs during laying and incubation, when the brooding female may be more vulnerable to terrestrial predators (Bergerud 1988). Although male survival was indeed greater than that of females during the nesting season in our study, this difference persisted after the nesting season (Figure 2.2). In fact, our best-supported model suggested that differences among all demographic groups were similar across seasons, with male survival higher than female survival throughout the year. This contrasts with results from Hannon et al. (2003), in which survival was similar for males and females outside of the nesting season.

Inconsistent differences between male and female survival estimates among studies may be partially attributable to the varied movement ecology of willow ptarmigan among study areas. In Scandinavia, where survival estimates have been found to be similar for males and females (Smith and Willebrand 1999), the largest seasonal movement observed was 33 km, with most movements substantially smaller (Hörnell-Willebrand et al. 2014). In contrast, seasonal movements of >100 km have been observed frequently in arctic (Irving et al. 1967, Weeden and Ellison 1968) and subarctic (Chapter 4) Alaskan populations. On average, female willow ptarmigan appear to exhibit substantially larger seasonal movements than males in Interior Alaska (Chapter 4). In Norway and Sweden, females also moved farther than males, but the magnitude of the difference was far less than in Alaska (Hörnell-Willebrand et al. 2014). Thus, if there is a survival cost associated with larger movements (e.g., due to energetic expense, increased exposure to predators, etc.), then a greater disparity in survival between the sexes would be expected in populations that exhibit greater differences

in movement distances.

Although differences in adult sex-specific survival rates vary among studies, survival rates of juvenile tetraonids are typically lower than those of adults (Hannon and Martin 2006). Lindström (1999) summarized studies of tetraonids that reported a range of 12–60% survival from the brood rearing stage through recruitment the following spring. Myrberget (1988) estimated that only 32% of juvenile willow ptarmigan survived to their first breeding season in Norway, as opposed to an annual adult (pooled sexes) survival estimate of 54%. Our estimates were similarly low for juveniles during this period (0.35 at remote sites; 0.24 at accessible sites).

These low annual survival rates of juvenile tetraonids are partially a consequence of low autumn survival (Hannon and Martin 2006). Our results appeared consistent with this in that monthly survival estimates dropped during the autumn dispersal season. However, the decrease was only moderate (Figure 2.2) and there was uncertainty associated with the season-specific estimates (probabilities of 87.8% and 65.4% that true survival during autumn dispersal was lower than that during brood-rearing at remote and accessible sites, respectively; 2.5). A potential factor to consider in interpreting temporal survival dynamics of juveniles is the selective disappearance of lower quality (i.e., frail) individuals during their first year of life (Vaupel et al. 1979, Vaupel and Yashin 1985, McNamara and Houston 1996, Cam and Monnat 2000, Lindberg et al. 2013). Population-level survival estimates during spring are conditional on the individuals in the spring sample not experiencing mortality prior to that time. If variation in individual quality results in heterogeneity in survival during autumn and winter, then the spring sample of ptarmigan may be composed of a greater proportion of high-quality individuals that exhibit higher survival probabilities. Thus, observed survival rates during spring may be higher in the presence of individual heterogeneity than if individual level variation is not associated with survival propensity. Further research on individual heterogeneity in life history traits of ptarmigan is needed to disentangle this explanation from the potential influence of extrinsic factors on temporal variation in juvenile

survival probability.

2.6.2 Spatial and Temporal Variation in Survival

Survival rates in our study differed notably between remote and accessible sites (Figures 2.2 and 2.3) and were consistent with estimated annual survival for a mixed-sex sample of willow ptarmigan under different harvest regimes in Norway (Sandercock et al. 2011). There, estimated annual survival probability for radio-marked ptarmigan was 0.54 ± 0.08 (SE) in unhunted areas, as opposed to 0.30 ± 0.05 in hunted areas (Sandercock et al. 2011). Smith and Willebrand (1999) reported similar estimates of 0.55 and 0.35 for their mixed-sex sample of adults in areas with no harvest and harvest, respectively. Our estimates of male survival were consistent with this past work, but both female and juvenile survival were lower in our study in both remote and accessible areas. Overall, the differences in survival related to harvest pressure suggest that there may be an additive component of harvest mortality across sex and age classes. Pedersen et al. (2004) similarly concluded that harvest mortality had a strong additive component across demographic groups in a Norwegian population (but see Sedinger 2010).

This idea was further supported by the way in which seasonal variation in survival was associated with the spatial distribution of birds. Seasonal movements in our study area were large enough to result in spatial mixing of birds from accessible and remote sites during part of the year, which was consistent with a spatial influence on survival. Specifically, seasons in which ptarmigan in the study area were clearly delineated into accessible and remote locations (nesting, brood rearing), survival was lower for birds at accessible locations. Similarly, when birds were initiating dispersal from breeding/natal territories, but were still relatively close, survival was lower at accessible sites. In contrast, birds from accessible breeding/natal territories were not spatially segregated from those with remote breeding/natal territories during winter and pre-breeding, and survival was similar for all birds during these periods, further suggesting that survival is negatively associated with presence at accessible sites.

An apparent exception to this pattern was that ptarmigan returned to the vicinity of breeding/natal territories in the late pre-breeding season, during which time we estimated survival to be similar for birds from accessible and remote sites. However, this occurred at the end of the pre-breeding season, when the ptarmigan hunting season was closed, so birds at accessible territories were not subjected to harvest.

There are several possible alternative explanations for lower annual survival rates of ptarmigan in accessible areas. We designed the sampling in our study to address potential differences between areas that receive substantial hunting pressure and those that do not. However, in our study, the impact of hunting was confounded with other potential impacts associated with the accessibility of sites (e.g., vehicular collisions, non-hunting human recreation, predator abundance). We documented vehicular collisions incidentally for both radio-marked and non-radio-marked ptarmigan when travelling on the primary road corridor during the study, but the actual rates of vehicular collision were unknown. Recreational disturbance may have direct or indirect effects on grouse (Thiel et al. 2007, Storch 2008, Moss et al. 2014). Recreation not associated with hunting was common in the accessible study sites and could possibly have contributed to ptarmigan mortality, especially during the breeding and brood-rearing seasons (Moss et al. 1990), but little evidence exists for population-level impacts of recreational disturbance on grouse species (Storch 2013). Data on relative predator abundance within our study sites were unavailable, but several species were present, including terrestrial (red fox; coyote, *Canis latrans*; wolverine, *Gulo gulo*; lynx, *Lynx canadensis*; marten, *Martes americana*; Pozzangherra et al. 2016) and avian (gyrfalcon, *Falco rusticolus*; peregrine falcon, *Falco peregrinus*; golden eagle, *Aquila chrysaetos*; northern harrier, *Circus cyaneus*; long-tailed jaeger, *Stercoarius longicaudus*; great-horned owl, *Bubo virginianus*; great gray owl, *Strix nebulosa*; snowy owl, *Bubo scandiacus*; short-eared owl, *Asio flammeus*; common raven, *Corvus corax*) species. Increased red fox abundance is associated with roadways in other regions (Ruiz-Capillas et al. 2013, Planillo et al. 2018), and foxes and other mesocarnivores are important predators of ptarmigan during nesting

(Hannon and Barry 1986, Hannon et al. 1998), possibly explaining our lower survival rates at accessible sites during the nesting season (Figure 2.2).

Despite these potential alternative mortality factors, ptarmigan harvest is known to be high in the accessible sites (Merizon et al. 2015), making it likely that reduced survival there was at least partially attributable to hunting. Moreover, the lack of difference in survival during the pre-breeding seasonat the end of which ptarmigan returned to spatially segregated territories but were not subjected to harvestprovides additional support for the hypothesis that harvest is a mechanism behind the reduced survival at accessible sites. As such, our results suggest that there may be an additive component of harvest mortality on ptarmigan survival in this system, due either to the magnitude or the timing of harvest. In addition, harvest mortality and non-harvest mortality may not be independent. High hunting pressure, and perhaps other forms of intensive disturbance, can increase non-harvest mortality in hunted areas (superadditive harvest response; Kokko 2001). For example, frequent flushing of ptarmigan in response to hunters may increase exposure and vulnerability to predators or lead to changes in habitat use (Brøseth and Pedersen 2011). We saw no evidence of compensation during subsequent seasons (Boyce et al. 1999), as seasonal estimates for ptarmigan from remote and accessible sites converged during the winter and pre-breeding seasons, resulting in lower annual survival for ptarmigan from accessible sites (Figure 2.2).

There are several potential explanations for the reduced survival during brood-rearing and autumn dispersal, including (1) increased avian predation due to raptor migration and dispersal, (2) molt-induced coloration mismatches with surroundings, (3) energetic stress resulting from active molt and dispersal locomotion, and (4) exposure to unfamiliar environments during dispersal movements (Hannon and Martin 2006). Fall raptor migration in the study area occurs in September and October, with peaks in golden eagle (*Aquila chrysaetos*) and rough-legged hawk (*Buteo lagopus*) migration occurring in October (i.e., during the autumn dispersal season; McIntyre et al. 2008, McIntyre and Lewis 2016), and seasonal increases in ptarmigan predation often coincide with raptor migration (Hudson et al. 1997,

Smith and Willebrand 1999, Hannon et al. 2003, Sandercock et al. 2011). Moreover, ptarmigan are an important food source for golden eagles in the vicinity of the study area (McIntyre and Adams 1999, McIntyre and Schmidt 2012), and large numbers of eagles migrate through this region of Alaska (McIntyre et al. 2008, McIntyre and Lewis 2016). Seasonally varied plumages facilitate effective crypsis within the drastically different background colors of boreal and arctic seasons (Baker and Parker 1979). Mismatches between plumage coloration and ground coloration during molt may increase vulnerability to predation during autumn, and the molt process makes autumn an energetically challenging period for ptarmigan (West 1968). Moving through unfamiliar terrain may also increase predation risk for dispersing tetraonids (Yoder et al. 2004); however, elucidating the role of each of these factors will require research on both the proximate and ultimate causes of ptarmigan mortality.

2.6.3 Local Population Stability

Regardless of the causal mechanism, our population projection model suggested that the survival rate at accessible sites was sufficiently low as to result in a population that is unsustainable without net immigration ($\hat{\lambda} = 0.71$ [95% CrI: 0.44–0.96]). In contrast, survival rates at remote sites were probably adequate to allow some population growth and/or emigration ($\hat{\lambda} = 1.05$ [95% CrI: 0.82–1.28]). However, the latter conclusion was accompanied by substantial uncertainty, with a 63% probability of $\lambda > 1$ at remote sites (as opposed to a 96% probability of $\lambda < 1$ at accessible sites).

These projections for lambda are dependent on the assumption that it is reasonable to characterize reproductive rates as uniform across study sites. If local compensation for lower survival occurred in the form of increased reproduction at accessible sites, then these projections would be negatively biased. We assumed a constant reproductive rate primarily because the sample of reliable brood counts obtained was limited in size when partitioned by site-type ($n_{\text{remote}} = 40$, $n_{\text{accessible}} = 22$). However, if we had estimated reproductive rates separately at remote and accessible sites, then our estimated mean number of offspring per

female would have been 4.2 and 3.1, respectively. These reproductive estimates would have increased the disparity in projected population growth rates between remote and accessible sites. A plausible mechanism for such a difference in reproductive rates exists in that successfully reproducing adults may be more vulnerable to harvest (Asmyhr et al. 2012), and a resulting shift in age structure to younger breeders at accessible sites could yield reduced chick production (Hannon and Zwickel 1979, Zwickel 1982, Smyth and Boag 1984, Bergerud 1988, Ellison 1991). Thus, our treatment of reproduction as spatially uniform provides a conservative assessment of spatial variation in ptarmigan population dynamics during the study period, and it suggests that compensatory immigration into accessible areas may be important for the viability of accessible breeding populations. This source-sink mechanism for sustaining locally exploited populations has been suggested for other ptarmigan populations (Smith and Willebrand 1999), as well as other hunted species (e.g., ruffed grouse, *Bonasa umbellus*, Small et al. 1991; greywing francolin, *Francolinus africanus*, Little et al. 1993; lynx, *Lynx canadensis*, Slough and Mowat 1996; culpeo foxes, *Pseudalopex culpaeus*, Novaro et al. 2005; cougars, *Puma concolor*, Robinson et al. 2008), suggesting that metapopulation processes may play an important role in maintaining local breeding populations in heavily hunted areas (Hanski 2001).

An important caveat when interpreting results from any study that involves marking wildlife is the potential effect of the marks on individuals in the study. Our survival inferences were based exclusively on radio-marked birds, so if transmitter presence had deleterious effects on survival of the marked birds in our study, our estimates would be biased low. Some studies have inferred negative effects of radio-transmitters on tetraonid survival (Rothenmaier 1979, Marks and Marks 1987, Cotter and Grotto 1995, Caudill et al. 2014). However, these effects were associated with non-necklace-style transmitter mounts, conspicuously colored transmitters, or transmitters that were >3% of body mass. To our knowledge, previous investigators have found no measurable effect of necklace mounted radio-transmitters on tetraonid survival when transmitters were <3% of body weight (Cotter and Grotto 1995,

Gibson et al. 2013, Thirgood et al. 1995, Hagan et al. 2006, Palmer and Wellendorf 2007).

Another consideration when interpreting our results is study duration. Many ptarmigan populations exhibit dramatic fluctuations in size. These fluctuations are cyclical in at least some regions, with 8-11 yr cycles documented in North America (Bergerud 1970, Hannon and Barry 1986, Mossop 1988, Boutin et al. 1995), 3-4 yr cycles documented in Scandinavia (Hrnfeldt, 1978, Myrberget 1984), and 4-7 yr cycles in England and Scotland (MacKenzie 1952, Jenkins et al. 1963). Detailed estimates of vital rates throughout complete cycles have not been documented in North America and are scant in Europe. However, vital rates obviously do not remain constant throughout these cycles, as changes in abundance are a function of changes in survival, fecundity, immigration, and/or emigration. Results from a concurrent project adjacent to our study area suggested that the population was likely in a low phase during our study (Schmidt et al. 2018). Our study only covered a three-year window and thus may not be representative of survival processes throughout ptarmigan population fluctuations. For example, during a 20-yr study, Steen and Erikstad (1996) estimated annual survival rates of adult willow ptarmigan that varied from 0.37-0.68. Given reproductive rates in their study, they concluded that annual survival varied sufficiently that harvest would cause population declines in some years, whereas substantial harvest would be sustainable in other years. More generally, there is evidence that the impact of top-down forces (e.g., harvest, predation) may be more additive when populations are at low phases because there is less potential for compensation when negative density-dependence is not limiting a population (Nichols et al. 1984, Bartmann et al. 1992, Salo 2010, Péron 2013). This additive effect may be particularly pronounced for cyclical populations at low phases (Salo 2010). Moreover, community dynamics may result in greater predation pressure during lows in population fluctuations if prey populations are approximately synchronized and ptarmigan are alternative prey to another species (e.g., Angelstam et al. 1984, Breisjoberget et al. 2018)

Overall, our results are consistent with the hypothesis that seasonally and spatially con-

centrated harvest decreases annual survival probabilities of willow ptarmigan. Given the observational nature of the study, results should be considered suggestive and further work should be conducted to replicate and refine these conclusions. Nevertheless, these results suggest that metapopulation processes linking heavily hunted areas and unhunted refugia may be critical in maintaining breeding populations in the formerat least during low phases of population fluctuations. This may be useful to managers in delineating areas that are open to hunting and those that are closed, especially in regions, such as Alaska, where access corridors receive concentrated pressure from hunters. In addition, the temporal survival patterns we documented may be useful to managers in setting hunting seasons. In particular, focusing harvest in seasons during which seasonal movements have yielded spatially mixed distributions of ptarmigan may reduce the impact on local breeding populations in heavily hunted areas.

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2.9 Figures

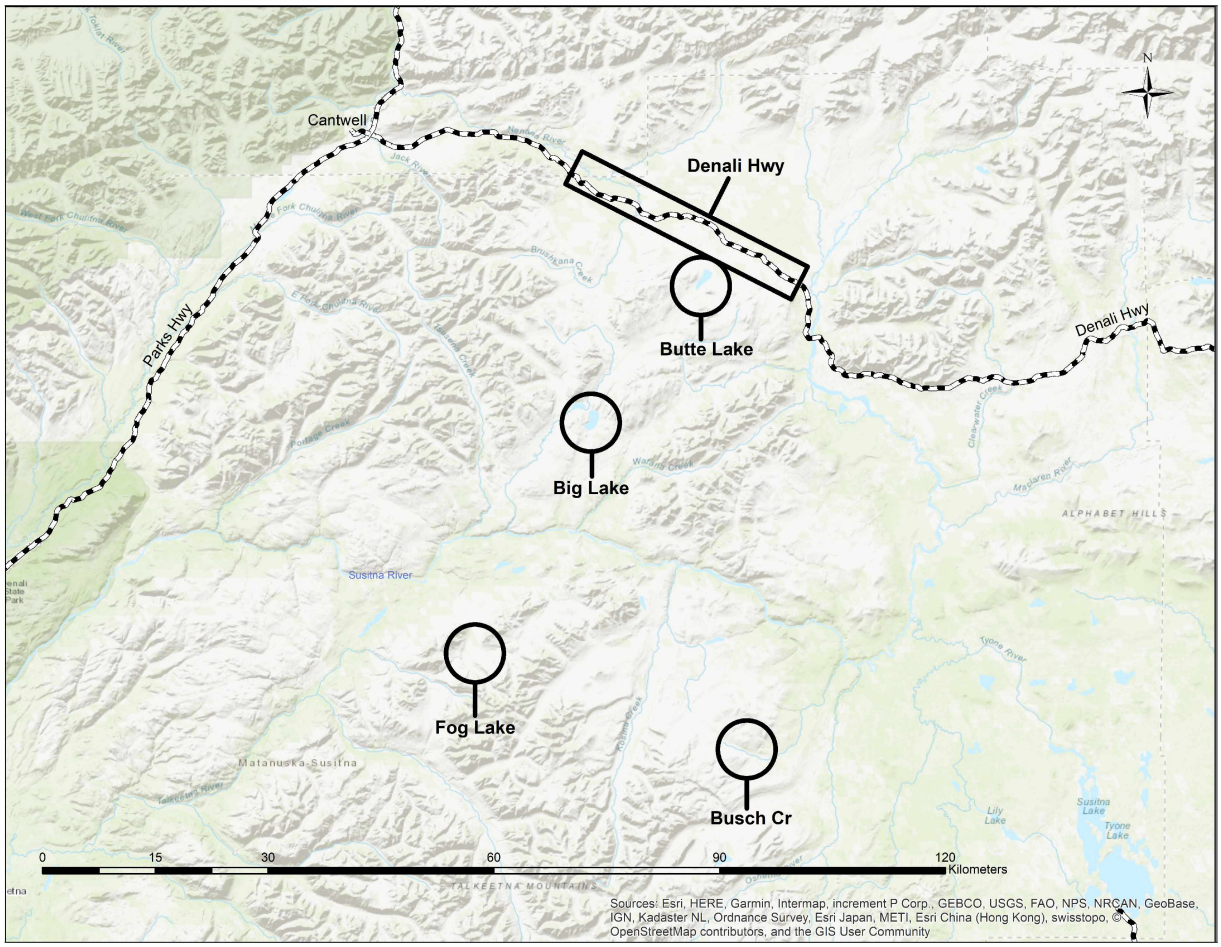

Figure 2.1: Willow ptarmigan (*Lagopus lagopus*) study sites in southern Interior Alaska, USA.

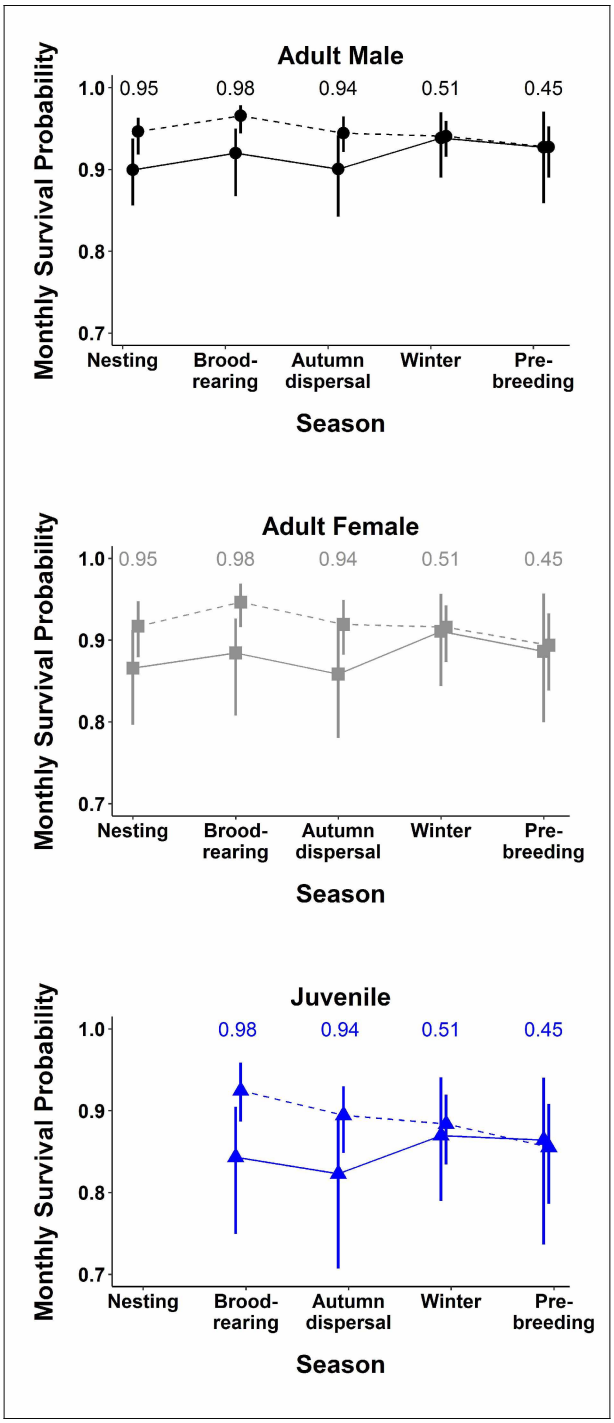

Figure 2.2: Seasonal estimates of monthly survival probability for willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA. Adults were $\geq$ 10 months old, whereas juveniles were $<$ 10 months old. Dashed lines represent remote sites and solid lines represent accessible sites. Point estimates are posterior means and error bars represent 95% credible intervals. Values at the top of each plot are the probabilities that the true values at remote sites were greater than those at the accessible sites for each season.

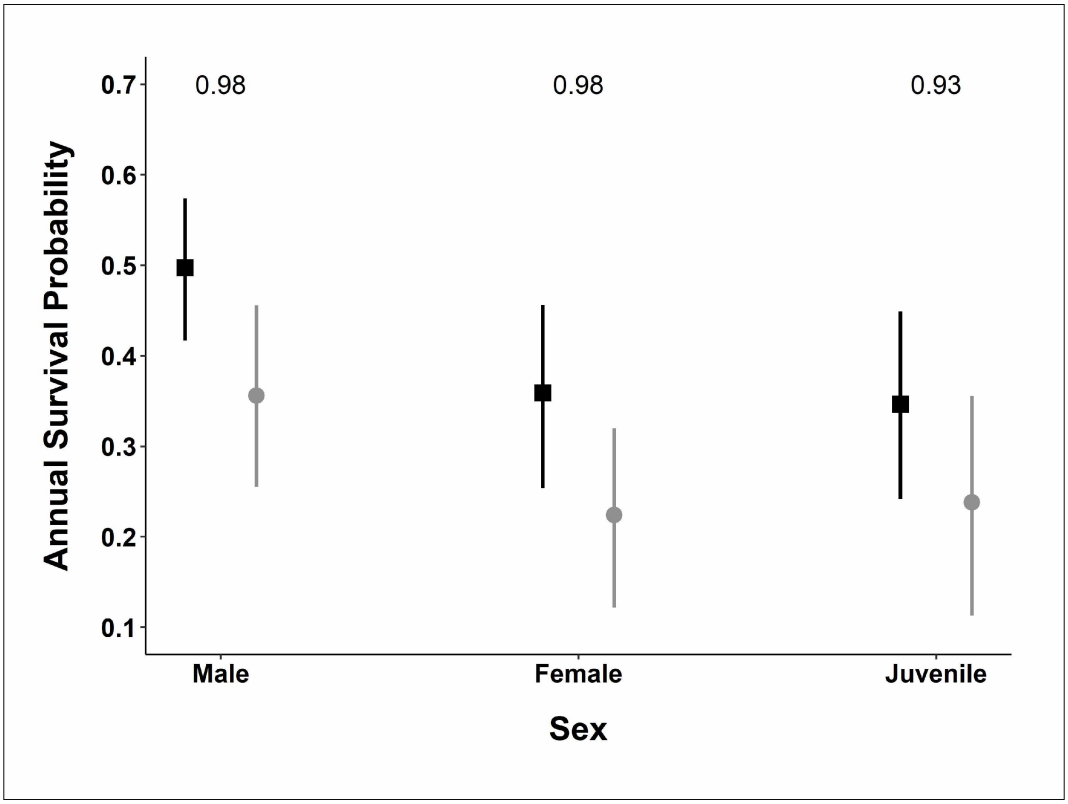

Figure 2.3: Estimates of annual survival probability for willow ptarmigan (*Lagopus lagopus*) from remote (black squares) and accessible (gray circles) sites in southern Interior Alaska, USA. Adults were ≥ 10 months old, whereas juveniles were < 10 months old. Annual survival estimates for juveniles apply to the period from early August through the end of April of the subsequent year ($\backsim$9 months). Point estimates are posterior means and error bars represent 95% credible intervals. Values at the top of the plot are the probabilities that survival at remote sites was greater than that at the accessible sites for each demographic group.

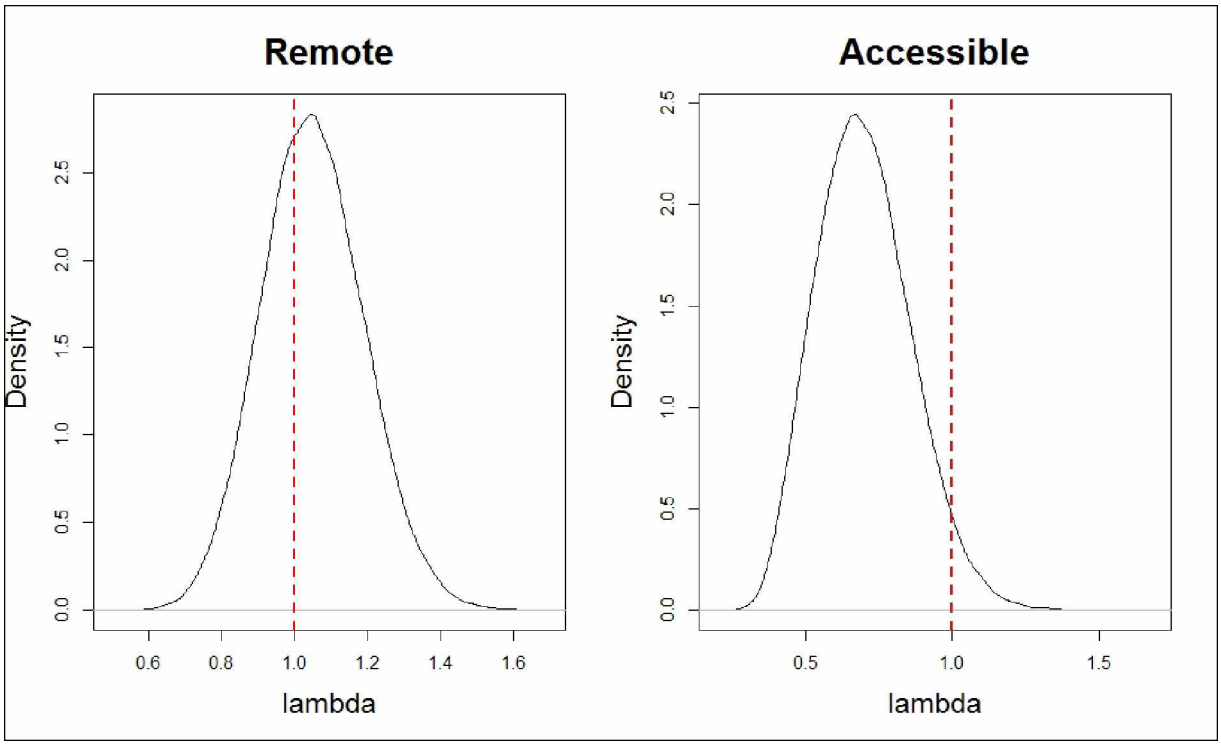

Figure 2.4: Derived probability densities for the finite rate of increase (λ) of willow ptarmigan (*Lagopus lagopus*) populations at remote sites with little or no hunting (Remote) and heavily hunted accessible sites (Accessible) in Alaska, USA.

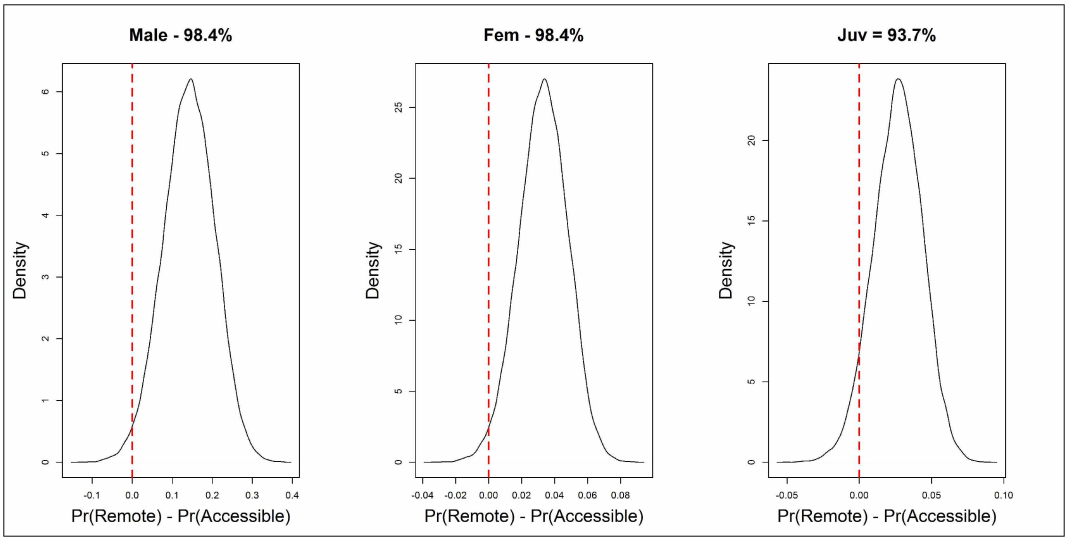

Figure 2.5: Derived probability densities for the differences in annual survival of willow ptarmigan (*Lagopus lagopus*) at remote sites with little or no hunting (Remote) and heavily hunted accessible sites (Accessible) in southern Interior Alaska, USA, for each demographic group (adult male, adult female, juvenile). The value at the top of each plot is the proportion of each probability density that is greater than zero, which is equivalent to the estimated probability that survival at remote sites is greater than survival at accessible sites for that demographic group.

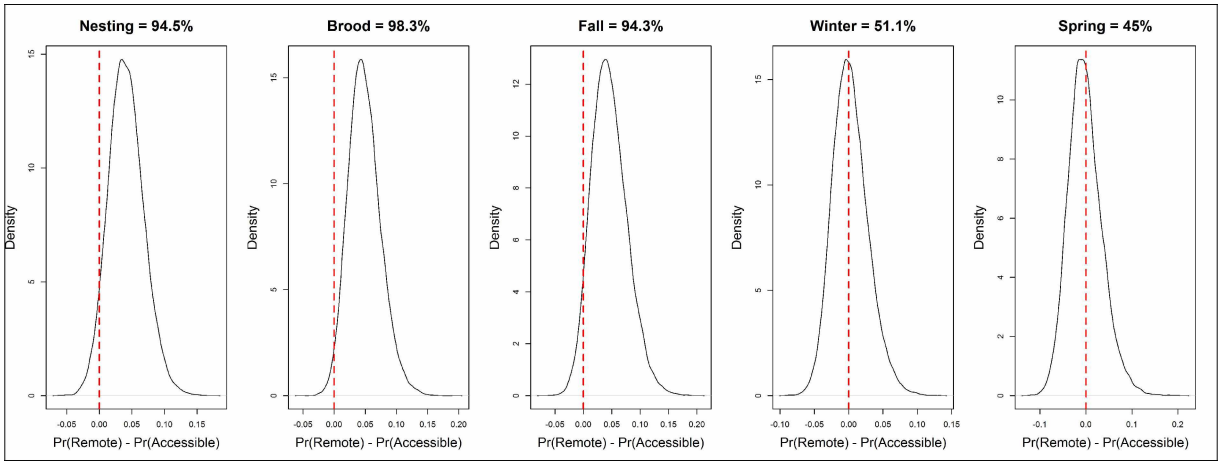

Figure 2.6: Derived probability densities for the differences in seasonal survival of willow ptarmigan (*Lagopus lagopus*) at remote sites with little or no hunting and heavily hunted accessible sites in southern Interior Alaska, USA. The value at the top of each plot is the proportion of each seasonal probability density that is greater than zero (denoted by the dashed red line), which is equivalent to the estimated probability that survival at remote sites is greater than survival at accessible sites for each season.

2.10 Tables

Table 2.1: Characteristics of the seasons delineated in modelling temporal variation in survival of willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA.

Season	Months within season	Season characteristics
Nesting	May, June, July	Territory fidelity and defense Transition to summer plumage Egg laying Incubation Early brood-rearing
Brood-rearing	August, September	Hunting in accessible areas Brood-rearing Early diurnal raptor dispersal/migration
Autumn dispersal	October, November	Hunting in accessible areas Aggregation into sexually segregated flocks Initiation of seasonal movements Transition to winter plumage Late diurnal raptor dispersal/migration
Winter	December, January, February	Hunting in accessible areas Winter roaming in sexually segregated flocks Females distributed farther from breeding territories than males
Pre-breeding	March, April	Hunting in accessible areas (March only) Transition to spring plumage Dissolution of sexually segregated flocks Return to vicinity of breeding territory (April) Males exhibit transient territoriality (April)

Table 2.2: Probabilities of monthly survival differing among seasons for willow ptarmigan (*Lagopus lagopus*) at remote sites with little or no hunting (Remote) and heavily hunted accessible sites (Accessible) in southern Interior Alaska, USA. Probabilities were derived from the posterior densities of each individual season parameter. Differences among seasons are the same within each demographic group because inference was based on an additive effect of age/sex in the survival model. Values are the probability that the season in the column header is greater than the season in each row below it.

	Remote					Accessible				
	Nesting	Brood-rearing	Autumn dispersal	Winter	Pre-breeding	Nesting	Brood-rearing	Autumn dispersal	Winter	Pre-breeding
Nesting	-	0.895	0.551	0.423	0.217	-	0.653	0.487	0.857	0.746
Brood-rearing	0.104	-	0.122	0.061	0.024	0.347	-	0.346	0.758	0.638
Autumn dispersal	0.449	0.878	-	0.360	0.169	0.513	0.654	-	0.842	0.745
Winter	0.577	0.939	0.640	-	0.257	0.143	0.242	0.158	-	0.416
Pre-breeding	0.783	0.976	0.831	0.743	-	0.254	0.362	0.255	0.584	-

Chapter 3: Reduced Breeding Densities Associated with Spatially Concentrated Harvest of Willow Ptarmigan in Alaska[2]

3.1 Abstract

The effects of human exploitation on wildlife have long drawn considerable attention from researchers and managers. Understanding the impacts of harvest on wildlife populations is fundamental to both theoretical wildlife science and applied wildlife management. Demographic compensation plays a key role in models of wildlife population dynamics and in developing harvest strategies. However, the degree and form of compensation in a given population depends on its particular ecological and life history characteristics, as well as the timing and magnitude of harvest. Consequently, substantial variation exists in compensatory potential among populations, and it cannot be assumed that a particular population is capable of compensating for harvest. This underscores the importance of population-specific assessments of responses to harvest. We examined the hypothesis that concentrated hunting pressure in road-accessible areas reduces subsequent breeding season densities of a highly valued upland game species, the willow ptarmigan (*Lagopus lagopus*), in Alaska, USA. We estimated the breeding season densities of ptarmigan territories at sites within heavily hunted access corridors and at remote sites in similar habitats with little or no hunting pressure. The site-specific parameter estimates indicated that the two remote sites (34–80 km from nearest access road) were higher in density ($\hat{\beta}$ = 1.05, SE = 0.23, $P < 0.001$ and $\hat{\beta}$ = 1.37, SE = 0.30, $P < 0.001$) than the most accessible site (0–1.6 km from access road). The second most accessible site (1.6-7.0 km from access road) also had higher density ($\hat{\beta}$ = 0.67, SE = 0.28, $P = 0.02$) than the most accessible site. Two habitat-proxy covariates, distance to water and elevation (modelled as smoothed effects), exhibited strong associations with the density of ptarmigan territories ($F = 14.17$, $P < 0.001$ and $F = 2.44$, $P = 0.04$, respectively). Resulting realized density estimates were substantially higher at remote

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sites (5.3–5.8 territories per km^2) than at accessible sites (1.8–3.7 territories per km^2), as were predicted densities when habitat covariates were held constant at their median values (remote: 8.7–12.7 territories per km^2, accessible: 2.9–6.3 territories per km^2). These results suggest a possible additive effect of spatially concentrated harvest on local breeding densities. We recommend that managers carefully monitor ptarmigan populations in heavily hunted, accessible corridors to avoid unsustainable declines in breeding density and the concomitant loss of hunting and viewing opportunity.

3.2 Introduction

A perennial question in the study of exploited populations is how harvest impacts subsequent abundance. Numerous studies have investigated the effects of harvest on particular species and populations (e.g., Burnham and Anderson 1984, Small et al. 1991, Williams et al. 2004, Hamel et al. 2006, Cooley et al. 2009). Results clearly indicate that harvest effects vary widely and depend on the ecological and life history characteristics of a given population (e.g., Bergerud and Huxter 1969, Sendinger et al. 2007, Turgeon and Kramer 2012, Lindberg et al. 2013), as well as the timing and magnitude of harvest (Boyce et al. 1999, Kokko and Lindström 1998, Ratikainen et al. 2008, Blomberg 2015, Caudill et al. 2017). Some populations are able to compensate for harvest mortality with decreased natural mortality after the hunting season (Roseberry and Klimstra 1984, Bartmann et al. 1992, Sandercock et al. 2011), through increased reproductive output or recruitment (Myrberget 1984, Swenson 1985, Bro et al. 2003), or with increases in local immigration (Pulliam 1988, Smith and Willebrand 1999, Martin et al. 2000). In the absence of some compensatory mechanism, harvest mortality will cause reduced abundance in the harvested population (Anderson and Burnham 1976). Species on the r-selected end of the life history spectrum (low survival, short longevity, early reproduction, high fecundity) are typically considered more capable of compensation than those on the K-selected end of the spectrum (high survival, greater longevity, late onset of reproduction, low fecundity), because of their greater potential for compensatory

reproduction, recruitment, and survival (McCullough 1990, Stearns and Kawecki 1994, Coulson et al. 2000, Péron 2013). However, this simplistic model of compensatory potential is insufficient for explaining observed responses to harvest in many populations, and variation in population-level responses to harvest, even within species, underscores the importance of making population-specific assessments of harvest impacts.

In Alaska, as elsewhere in the Holarctic, willow ptarmigan (*Lagopus lagopus*) are highly valued as an upland gamebird, for both subsistence and recreational hunting (Hannon et al. 1998, Merizon et al. 2015). Willow ptarmigan establish breeding territories in late April and May, which they defend against conspecifics (Hannon et al. 1998). Adults typically form monogamous pair bonds (although some males are polygynous), and both sexes care for the young until they disperse from their natal territories in autumn (Weeden 1963, Martin and Cooke 1987). During the breeding season, willow ptarmigan are sedentary and territorial; however, they can move relatively long distances from territories outside of the breeding season, typically in non-territorial, sex-segregated flocks (Weeden 1964, Irving et al. 1967, Mossop 1988). Ptarmigan hunting seasons tend to be long in Alaska, often open from early August through the following spring (typically ending in March but as late as June in some areas). Thus, during the early hunting season, ptarmigan are at or close to breeding territories and subsequently they can be far away due to migratory or nomadic seasonal movements before returning to breeding territories the following spring. Although willow ptarmigan are widespread and relatively abundant throughout much of the state (Weeden 1965), access to ptarmigan populations in most regions of Alaska is difficult. Consequently, corridors along Alaskas limited road system receive heavy use by hunters. Harvest of willow ptarmigan is high along the portions of these road-access corridors that traverse ptarmigan habitat (Merizon et al. 2015), but the impact of this spatially concentrated harvest on ptarmigan populations is unclear. Seasonal movements away from breeding territories reduce exposure to harvest for some portion of accessible populations and thereby contribute to uncertainty about the impact concentrated ptarmigan harvest in accessible corridors has on

local breeding populations.

Our objective was to estimate densities of willow ptarmigan territories at road-accessible sites, with high-levels of seasonal harvest, and at remote sites with little to no harvest. We examined the hypothesis that concentrated hunting pressure in road-accessible areas reduces local breeding season densities. We predicted that accessible sites, where there is substantial hunting pressure from August through March, would have lower densities of ptarmigan territories during the breeding season than remote sites with low hunting pressure. Identifying harvest effects on breeding densities could have important implications for harvest management in heavily hunted areas.

3.3 Study Area

We conducted our study in the southern Alaska Range and northern Talkeetna Mountains in southern Interior Alaska, USA (Figure ??). Within this region, we designated four survey sites, which differed in their degrees of accessibility. Elevations at the survey sites ranged from 850-1,230 m. These sites contained a mix of barren rocky slopes, open tundra-dominated hills, shrub tundra, and riparian areas. Shrub species were primarily dwarf birch (*Betula nana, B. glandulosa*), alder (*Alnus* spp.), and willow (*Salix* spp.). Subalpine stands of spruce (*Picea* spp.) and taller stands of dwarf birch were typical at lower elevations.

Ptarmigan hunting pressure varied with distance of survey sites from the Denali Highway (Figure ??). The Big Lake and Fog Lake sites (hereafter, 'remote' sites) were located 34 - 80 km from the Denali Highway and were accessible primarily by small aircraft. The Butte Lake and Denali Highway sites (hereafter, 'accessible' sites) were within 7 km of the Denali Highway, which is accessible by highway vehicle. The Butte Lake site was located near the Denali Highway and received substantial use by hunters on ATVs, snowmobiles, and on foot. The Denali Highway site contained the highway and the area within 1.6 km of the highway. We based this 1.6 km delineation on harvest research conducted on ptarmigan elsewhere in Alaska (Weeden 1972). Use of the accessible study sites was substantial and included

ptarmigan hunting, as well as non-hunting recreation (e.g., hiking, all-terrain vehicle use, snowmobile use). Conversely, human use of the remote sites was extremely limited. The ptarmigan hunting season in the study area ran from 10 August through 31 March during the years of this study.

3.4 Methods

3.4.1 Field Methods

During May of 2014 and 2015, we conducted surveys using line transect distance sampling (Buckland et al. 2001) at each site to estimate willow ptarmigan breeding territory density. Individual observers walked transects and counted all territorial male ptarmigan detected. We focused on territorial males because they conspicuously defend breeding territories during May, and thereby provide a way to enumerate breeding territories. For each ptarmigan that was detected, observers recorded: (1) the coordinates of the observer location (recorded with a global positioning system receiver), (2) the distance and bearing from observer to ptarmigan (measured with a laser rangefinder and compass, respectively), (3) the behavior of the ptarmigan, and (4) time of observation. At each site, 8 - 10 parallel transects (1.5-3.0 km long) per year were spaced systematically by 800 m in shrub-tundra habitats between 822 m and 1,158 m (2,700-3,800 ft) of elevation, which was known *a priori* to contain appropriate breeding habitat for willow ptarmigan.

3.4.2 Data Analysis

We analyzed survey data using density surface models (Miller et al. 2013). Density surface models employ a spatially explicit two-stage approach that begins with fitting a classical parametric detection function based on observation distances from a transect line (Buckland et al. 2001). However, rather than using the detection function to correct for imperfect detection at the scale of the transect, transects are partitioned into contiguous segments. After parameters of the detection function are estimated, the fitted function is

used to correct counts at the segment scale. These corrected counts are then used to estimate the effects of segment-level spatial covariates on density in the frameworks provided by generalized additive models (Wood 2006) or generalized linear models (McCullagh and Nelder 1989). Uncertainty in the fitted detection function can be incorporated into uncertainty in the abundance estimates via one of several variance propagation methods (Miller et al. 2013).

We right truncated detection data at 300m to avoid numerical problems that can arise in attempting to fit the tail of detection functions (Buckland et al. 2001). We then fit a half-normal detection function to the remaining data and included time of day and observer as covariates on the scale parameter (Figure ??). Transects were partitioned into segments that were 600 m wide and approximately 600 m long, resulting in approximate squares that corresponded with the survey strip half-width after truncation of the detection function at 300 m.

We then used a generalized additive mixed model (GAMM) with a spatial autoregressive term and covariates for year (2014, 2015), site (Denali Highway, Butte Lake, Big Lake, Fog Creek), elevation, and distance to water (lakes, streams) to estimate abundance. We included elevation and distance to streams/lakes as habitat proxies because both variables are associated with variation in shrub structure and abundance (Viereck et al. 1992), which are fundamentally associated with willow ptarmigan occupancy and abundance (Weeden 1959, Weeden 1963, Schieck and Hannon 1993, Hannon et al. 1998, Wilson and Hannon 2008). The model was specified as

$$\log(\mathbb{E}[\hat{N}_i]) = \beta_0 + \beta_1 2015_i + \beta_2 \text{Butte}_i + \beta_3 \text{Big}_i + \beta_4 \text{Fog}_i + s(\text{Elevation}_i) +$$

$$s(\text{DistWater}_i) + \text{offset}(\text{Area}_i) + \text{AR}(1)$$

where $\mathbb{E}[\hat{N}_i]$ is the expected value of the abundance estimate for segment i (corrected for imperfect detection) modelled with a log link function, β_0 is an intercept term representing the effect of reference levels for year (2014) and site (Denali Highway), β_1 is the coefficient

for a year-specific indicator variable for 2015 (2015_i), β_2 is the coefficient for a site-specific indicator variable for Butte Lake (Butte_i), β_3 is the coefficient for a site-specific indicator variable for Big Lake (Big_i), β_4 is the coefficient for a site-specific indicator variable for Fog Creek (Fog_i), $s(\text{Elevation}_i)$ is a smooth term for the effect of Elevation, $s(\text{DistWater}_i)$ is a smooth term representing the effect of distance from water (lakes, streams), $\text{offset}(\text{Area}_i)$ is an offset term to account for minor variation in the area of segments, and AR(1) is a spatial autoregressive term with a lag of one. We fit the smooth terms in the model as thin-plate regression splines (Wood 2003) and we used a Tweedie distribution (Jorgensen 1987) with exponential parameter p = 1.1 as the response distribution.

After fitting models, we generated predicted density surfaces for each survey site. In generating predicted densities, an arbitrary buffer of 4 km was placed around the survey transects at each site. The area within each resulting polygon was partitioned into 100 m by 100 m cells to form a prediction grid. We removed lake surfaces and land area falling outside the range of sampled elevations from the resulting prediction grids in order to constrain inferences to the portion of covariate-space that was actually sampled. We placed an additional constraint on prediction grids at the Denali Highway and Butte Lake sites. The Denali Highway grid was limited to area within 1.6 km of the road itself. Conversely, the adjacent Butte Lake grid was constrained so that it only contained area > 1.6 km from the Denali Highway. We based the 1.6 km delineation on work done by Weeden (1972), in which he found that most ptarmigan harvest occurred within 1.6 km of road access.

We conducted all analyses in the R software environment (R Core Team 2017). Functions from the R packages Distance (Miller 2015), dsm (Miller et al. 2016), mgcv (Wood 2011), and tweedie (Dunn 2014) were used in the analysis.

3.5 Results

We surveyed a total of 164.1 km of transect during the study (16.7-23.5 km per site-year) and we detected 290 territorial male willow ptarmigan. Abundance estimates for each

study site (defined by bounds of the respective prediction grids; Figure ??) ranged from 73-665 ptarmigan territories with corresponding density estimates that ranged from 1.8-5.8 territories per km2 (Table 3.1). The effect of year was both small and poorly estimated (Table 3.2) but resulted in a slight increase in density estimates from 2014 to 2015. Despite the uncertainty in the year effect, we retained it in the model to account for the fact that sampling occurred during two separate breeding seasons. Parameter estimates for site effects indicated that densities at the Denali Highway site were lower than those of the other sites (Tables 3.1 and 3.2).

Within each site-year, density varied with habitat covariates (Table 3.2). Increasing distance from streams/lakes was negatively associated with ptarmigan territory density (Figure ??). Elevation exhibited a positive association with density up to approximately 950 m of elevation (Figure ??). Above 950 m, the effect of increasing elevation was negative. When holding both elevation and distance from lake/stream at their median values, the predicted densities were substantially higher at remote sites than at accessible sites (Figure ??).

3.6 Discussion

The effects of concentrated harvest on breeding ptarmigan densities are important to understand both for advancing theory of harvest and predator prey dynamics, and for application to harvest management. Here we found that densities of ptarmigan breeding territories were higher at remote sites, with little or no hunting pressure, than at accessible sites, with concentrated hunting pressure. These results are consistent with the hypothesis that concentrated hunting pressure in road-accessible areas affects subsequent breeding densities of ptarmigan. Densities at hunted sites were approximately 50% lower than at sites without harvest, suggesting that concentrated harvest may have substantial additive effects at the population level, with important management implications. Research in Alaska has not addressed the effect of concentrated harvest on willow ptarmigan breeding populations, but Weeden (1972) and McGowan (1975) did not detect changes in estimated breeding densities

of rock ptarmigan (*Lagopus muta*) following moderate levels of harvest elsewhere in Interior Alaska. As some of the first work in Alaska directly assessing the impacts of harvest on willow ptarmigan, our results suggest that managers should consider accessibility of populations when setting harvest regulations.

Our work is consistent with previous investigations that have found an inverse relationship between harvest and subsequent tetraonid breeding densities. Pedersen et al. (2004) found a negative relationship between harvest and annual population growth of willow ptarmigan after experimental harvest in Norway (however, see Sedinger et al. 2010 for criticism of this analysis). Kubisiak (1984) and Small et al. (1991) estimated lower densities of breeding ruffed grouse (Bonasa umbellus) in harvest units relative to control areas. Connelly et al. (2003) and Gibson et al. (2011) inferred negative effects of hunting on greater sage-grouse (*Centrocercus urophasianus*) population growth, although the former was disputed by Sedinger and Rotella (2005).

However, others have observed compensatory responses in tetraonids. Red grouse (*L. l. scoticus*) were thought to exhibit complete compensation with moderate harvest as a result of a large number non-territorial, local birds that assumed the territories of harvested individuals (Jenkins et al. 1963). Rock ptarmigan abundance, likewise, did not change appreciably after experimental harvest during years of high density (Weeden 1972, McGowan 1975). Similarly, Palmer and Bennet (1963) found no difference in numbers of ruffed grouse breeding in spring at adjacent hunted and non-hunted properties. Braun and Rogers (1971) also inferred no change in breeding density of white-tailed ptarmigan (*Lagopus leucura*) following moderate harvest. Conflicting inferences about the effects of harvest on breeding density may result from several possible factors, including timing of harvest, magnitude of harvest, phase of population fluctuation, or relative breeding densities.

Dramatic, temporal, and often cyclical fluctuations in ptarmigan density are observed in many regions (Bergerud 1970, Myrberget 1984, Hannon and Barry 1986, Mossop 1988, Boutin et al. 1995), so previously reported density estimates may vary based on the phase

of the fluctuations in which estimation occurred. Most studies, including this one, obtain only a snapshot of ptarmigan population states or dynamics, and thus miss the comprehensive picture of ptarmigan demographics through all fluctuation phases. Data from a neighboring study area suggest that we conducted this study during a low population phase (Schmidt et al. 2018), so the differences we observed among sites may not be representative of other phases. It is plausible that a greater number of non-territorial ptarmigan may be present to adopt the territories of harvested individuals when the population is not in a low phase, which could reduce the disparity in densities between remote and accessible sites. Consistent with this idea, young, non-territorial ptarmigan may be more abundant when ptarmigan populations are high (Jenkins et al. 1967, Moss et al. 1996) and territories of harvested ptarmigan may be occupied relatively quickly by non-territorial birds (McGowan 1975, Hannon 1983, Pedersen 1984). In addition, compensation may be more likely to occur when populations are high because these populations are more likely to be experiencing negative density dependence in vital rates, and thus should have greater potential to increase vital rates in response to density reductions (Nichols et al. 1984, Bartmann et al. 1992, Salo 2010, Péron 2013). Thus, additive effects of harvest on subsequent density may be stronger during low ptarmigan population phases, when vital rates are less constrained by density.

Published estimates of willow ptarmigan densities vary dramatically by location and year, and the degree of hunting pressure is not always clearly detailed. Although previous estimates are not available for Alaska, breeding densities elsewhere in North America have been estimated to be as low as 0.5 territories per km^2 (Bergerud 1970) and as high as 77 territories per km^2 (Mossop 1988). Similarly, in Scandinavia, reported densities ranged from 2-70 territories per km^2 (Marcström and Höglund 1980, Myrberget 1988). Our density estimates (1.8-5.8 territories per km^2) fall within the wide range of reported estimates from other studies but are far below the maximum densities reported.

Densities predicted for constant covariate values (Figure **??**) and densities estimated as a function of observed site characteristics (Table 3.1) provide complementary information on

the variation in willow ptarmigan density at the study sites, and they are consistent with one another in indicating higher densities at remote sites with low hunting pressure. The former depict relative density among sites while accounting for spatial covariate effects. In other words, if the distribution of habitat characteristics were identical among sites, then one would expect these predicted values to approximate the estimated number of territories for each site-year. In contrast, the latter estimates are conditional on the particular site-specific distribution of realized covariate values. In other words, these estimates depend on both the site-effect and the particular habitat characteristics of that site. Densities predicted for constant covariate values can be used in understanding the effects specific factors (e.g., harvest, habitat characteristics) have on density, whereas densities estimated using actual site characteristics can be used in monitoring numerical changes at focal locations.

We only used detections of male ptarmigan in our analysis primarily because the cryptic plumage and behavior of females limited sightability to a degree that precluded female density estimation. Males defend exclusive breeding territories during May (Weeden 1963), so the number of territorial males represents the number of breeding territories. Non-territorial ptarmigan (primarily juvenile males) seeking to establish a breeding territory for the first time will sometimes roam (either singly or in small groups) through the territories of established males. We excluded non-territorial males from our analysis on the basis of behavior (Moss 1972, Watson and Jenkins 1964) in order to base inference on a clearly defined population. In practice, there were few observations of non-territorial ptarmigan during the breeding seasons in our study, which is consistent with the notion that we conducted our study near a low population phase (Schmidt et al. 2018), as non-territorial ptarmigan appear to be more common during high phases (Jenkins et al. 1967, Moss 1972, Moss et al. 1996). Our observations of radio-marked males at the study sites suggested that most or all territorial males successfully paired with at least one female during 2014 and 2015. However, rigorous estimates of pairing and polygyny rates are not available for these study sites, so we were unable to estimate female density based on pairing rates. Moreover, polygyny rates

may be influenced by density (Hannon 1983), which further complicates potential efforts to correct for segments of the population that were not included in the estimation. Thus, the estimates in this study should be considered to apply strictly to the number of territorial male ptarmigan, which corresponds to the number of breeding territories, but not to the actual number of birds present. Nevertheless, differences in the total number of birds present at the study sites is likely approximately proportional to differences in the estimates provided here.

We used elevation and distance to water as surrogates for habitat structure and composition because quality vegetation data were not available across the study sites at the scale required. In shrub-tundra habitats, shrub density and structure are closely tied to water proximity and elevation, with higher shrub densities occurring adjacent to streams and lakes (Viereck et al. 1992). Similarly, at the upper end of the elevation range sampled, shrubs are sparse and small. Higher elevations are less commonly occupied by willow ptarmigan than elevations characterized by taller and more densely distributed shrubs. At the lower end of the elevation range sampled, shrubs are often tall and densely distributed, but stands of spruce are also common. We found that breeding ptarmigan densities peaked near 950 m (Figure ??), where vegetation is similar to habitat selected by breeding willow ptarmigan in other North American studies (Weeden 1959, Schieck and Hannon 1993, Hannon et al. 1998, Wilson and Hannon 2008).

The observational nature of this study imposes some limits to inference. Specifically, we cannot confirm a mechanistic link between harvest and breeding season densities. There are also confounding factors associated with the accessible sites, which complicate the interpretation of our results. Specifically, there were potential non-hunting impacts on ptarmigan at accessible sites, which included: (1) greater non-hunting recreation, (2) vehicular collisions, and (3) possibly higher predator densities. Recreational disturbance may have direct or indirect effects on grouse (Storch 2008), but population-level impacts of recreational disturbance have not been documented (Storch 2013). We documented ptarmigan mortalities from ve-

hicular collisions along the primary access road for the accessible study sites, but estimates of collision rates are unavailable. Several species of mammalian and avian predators occur within the survey sites (Pozzangherra et al. 2016). Red fox (*Vulpes vulpes*) predation, in particular, can impact ptarmigan populations (Hannon and Barry 1986, Moss et al. 1990, Lindström et al. 1994, Hannon et al. 1998, Munkabye et al. 2003), and fox abundance has been found to be positively associated with roads in some areas (Ruiz-Capillas et al. 2013, Planillo et al 2018). Any combination of these factors could have contributed to the reduced densities observed at accessible sites. Nevertheless, ptarmigan harvest was known to be high at the accessible sites (Merizon et al. 2015) and a companion study to this one estimated survival rates at our accessible sites to be notably lower than those at our remote sites (Chapter 2). Thus, despite any potential contribution of non-harvest factors, these results suggest that harvest mortality may have been at least partially additive to natural mortality and likely contributed to the lower densities of breeding territories at accessible sites.

Despite the observational nature of this study, results were consistent with the hypothesis that spatially concentrated harvest can negatively influence subsequent breeding densities of willow ptarmigan. Our estimates indicated that densities were substantially lower at accessible sites than at remote sites. A discrepancy in survival rates is a plausible mechanism for this difference in breeding densities, given that adult fidelity to breeding territories is high in willow ptarmigan (Brøseth et al. 2005, Hörnell-Willebrand et al. 2014). High rates of breeding site fidelity should limit the degree to which immigration can bolster low-density populations or compensate for low survival rates via a source-sink dynamic. In the absence of breeding dispersal (*sensu* Greenwood 1980), immigrants will primarily be pre-breeding juveniles dispersing from their natal territories (Greenwood and Harvey 1982). Spatial variation in reproductive rates is also a plausible, and perhaps complementary, mechanism for a difference in breeding densities. Further research is necessary to determine whether similar patterns occur outside of low population phases, and to what degree factors other than har-

vest may contribute to reduced densities in accessible areas. Future research would benefit from conducting manipulative harvest experimentation to better examine whether a causal link exists between harvest and breeding density.

Our results suggest that managers should carefully monitor ptarmigan populations in heavily hunted, accessible corridors to avoid unsustainable declines in breeding density and the concomitant loss of hunting and viewing opportunity. Management strategies that disperse the spatial concentration of harvest pressure may reduce the impact of hunting in heavily used access corridors. Alternatively, distributing hunting opportunity in accessible areas among disparate temporal periods could effectively reduce the concentrated use of any particular area. Further research on alternative harvest strategies for accessible populations with concentrated hunting pressure would aid in managing for sustainable ptarmigan yields.

3.7 Acknowledgments

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3.9 Figures

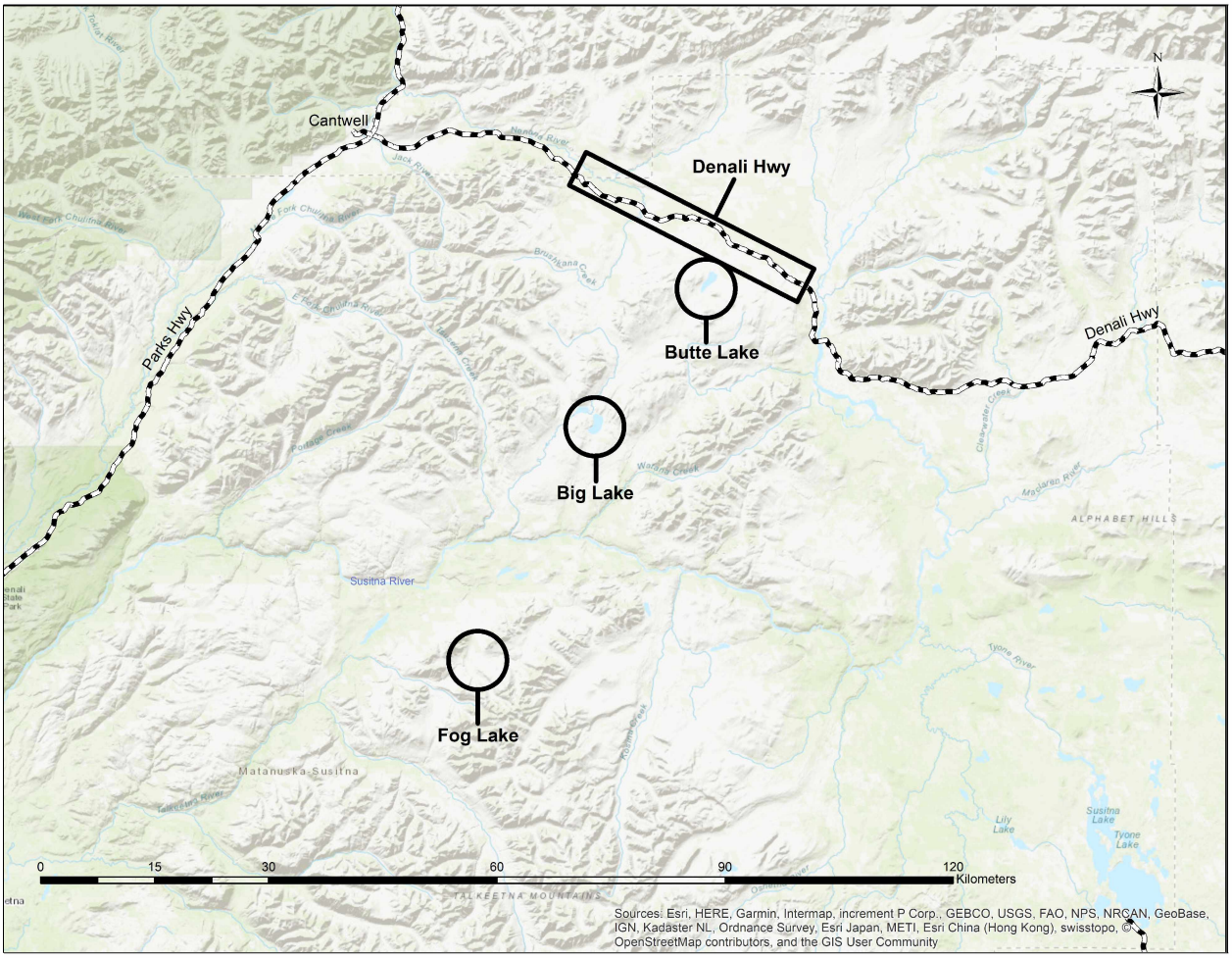

Figure 3.1: Sites at which distance sampling surveys were conducted to estimate density of willow ptarmigan (*Lagopus lagopus*) breeding territories during 2014 and 2015 in southern Interior Alaska, USA.

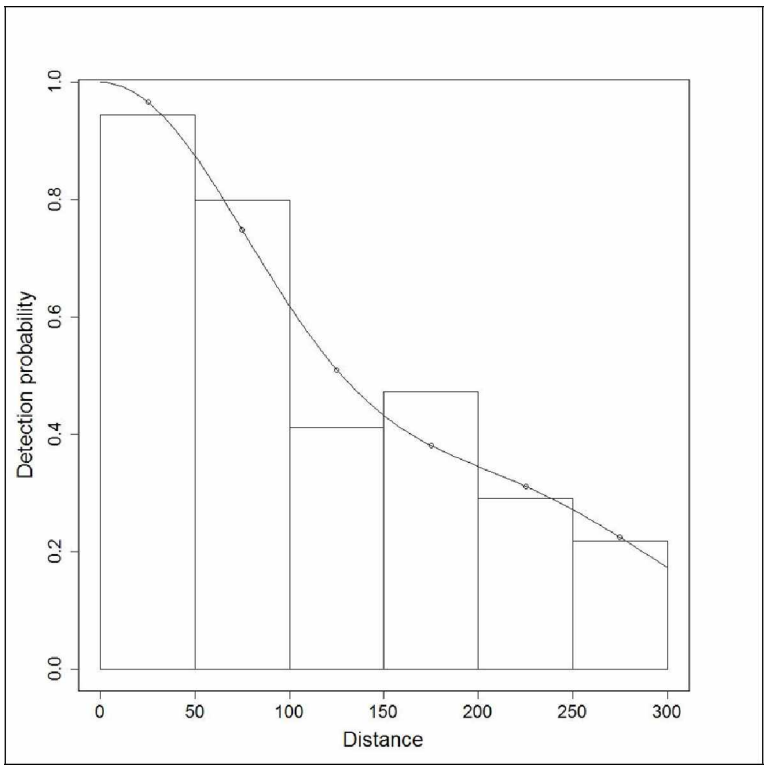

Figure 3.2: Fitted distance sampling detection function used to estimate density of willow ptarmigan (*Lagopus lagopus*) breeding territories during 2014 and 2015 in southern Interior Alaska, USA.

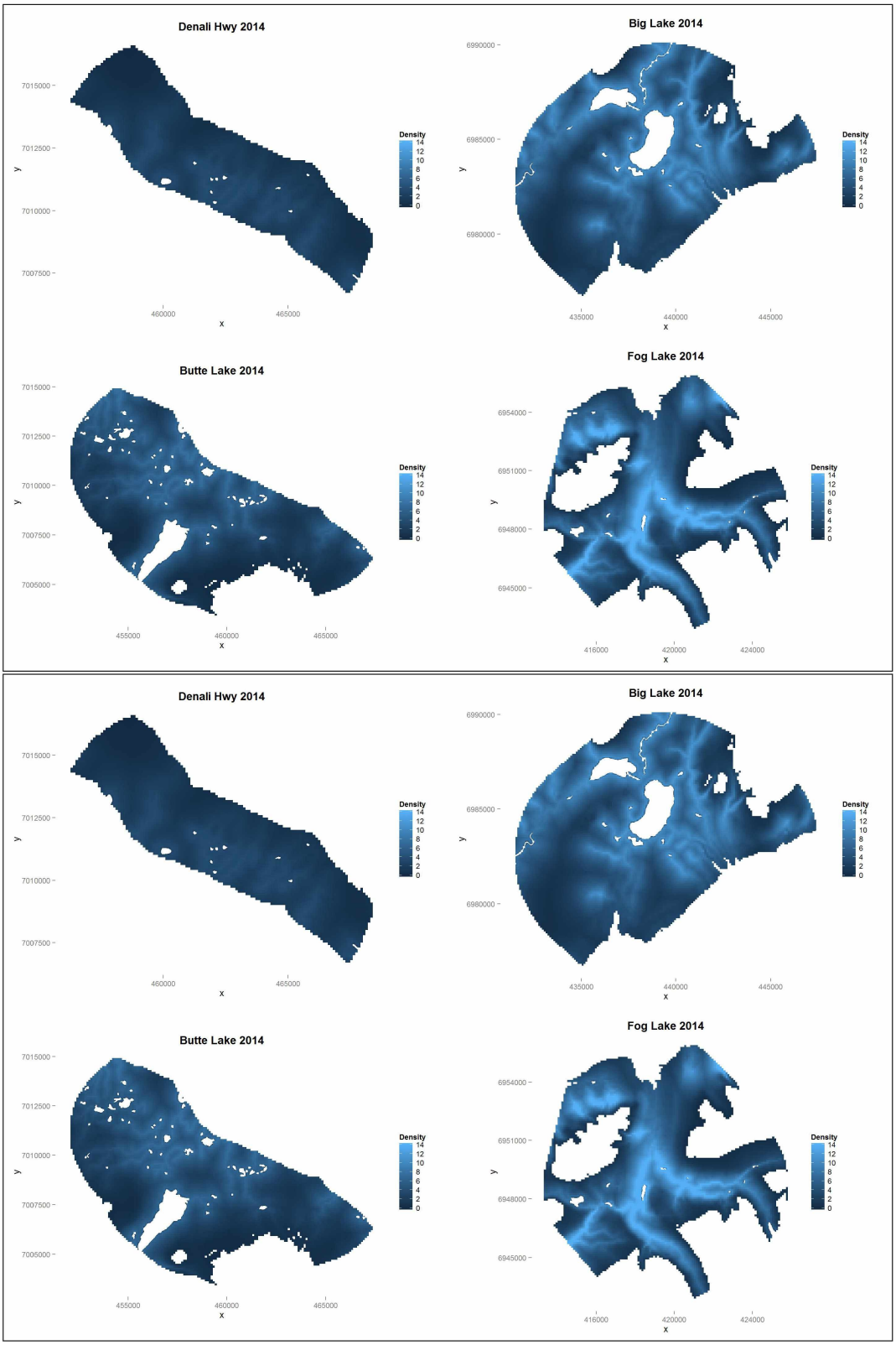

Figure 3.3: Predicted density surfaces depicting habitat-induced variation in the density of willow ptarmigan (*Lagopus lagopus*) breeding territories during 2014 and 2015 in southern Interior Alaska, USA as a function of spatial covariates.

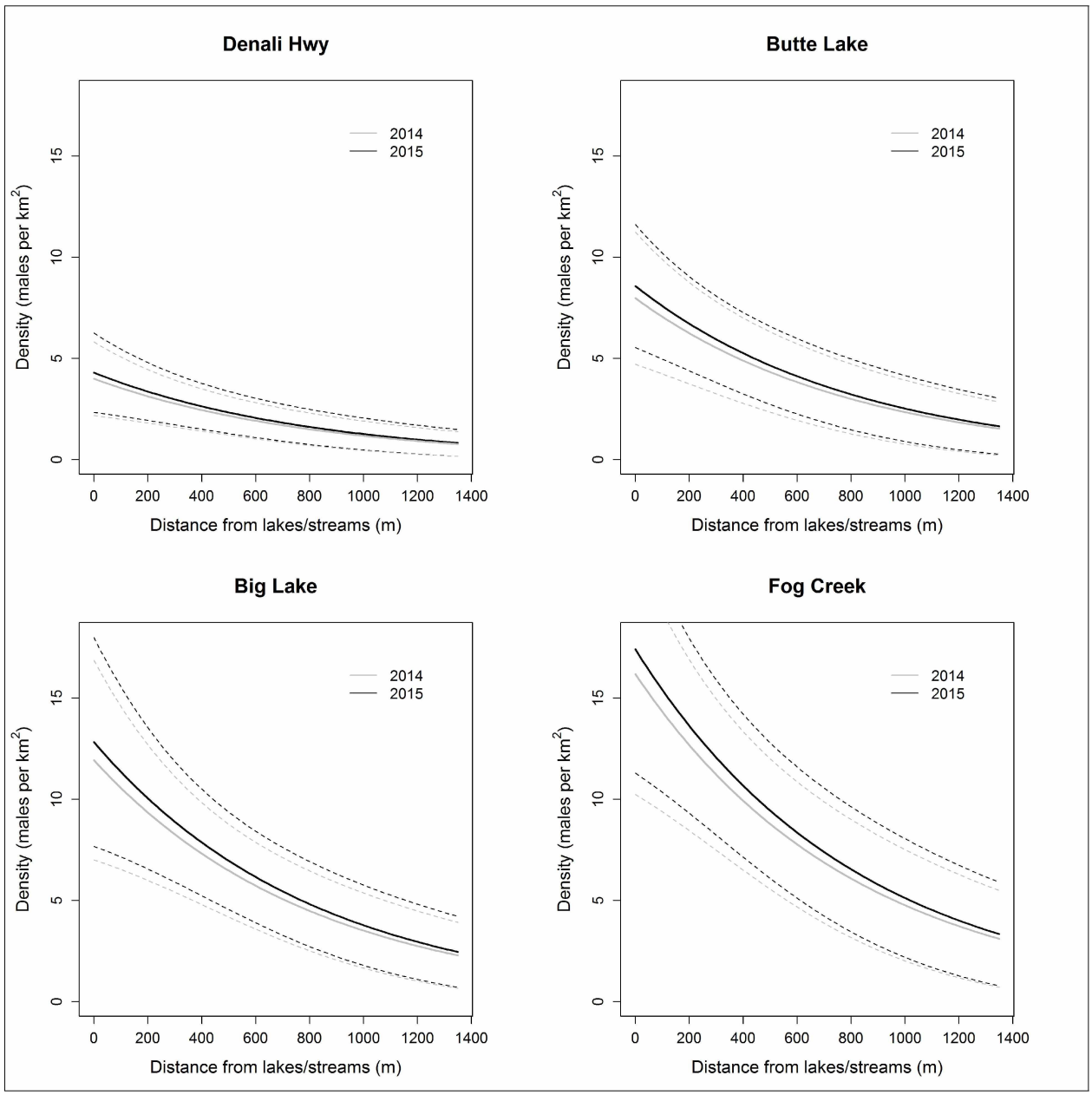

Figure 3.4: Estimated relationship between distance to water and density of willow ptarmigan (*Lagopus lagopus*) breeding territories in southern Interior Alaska, USA.

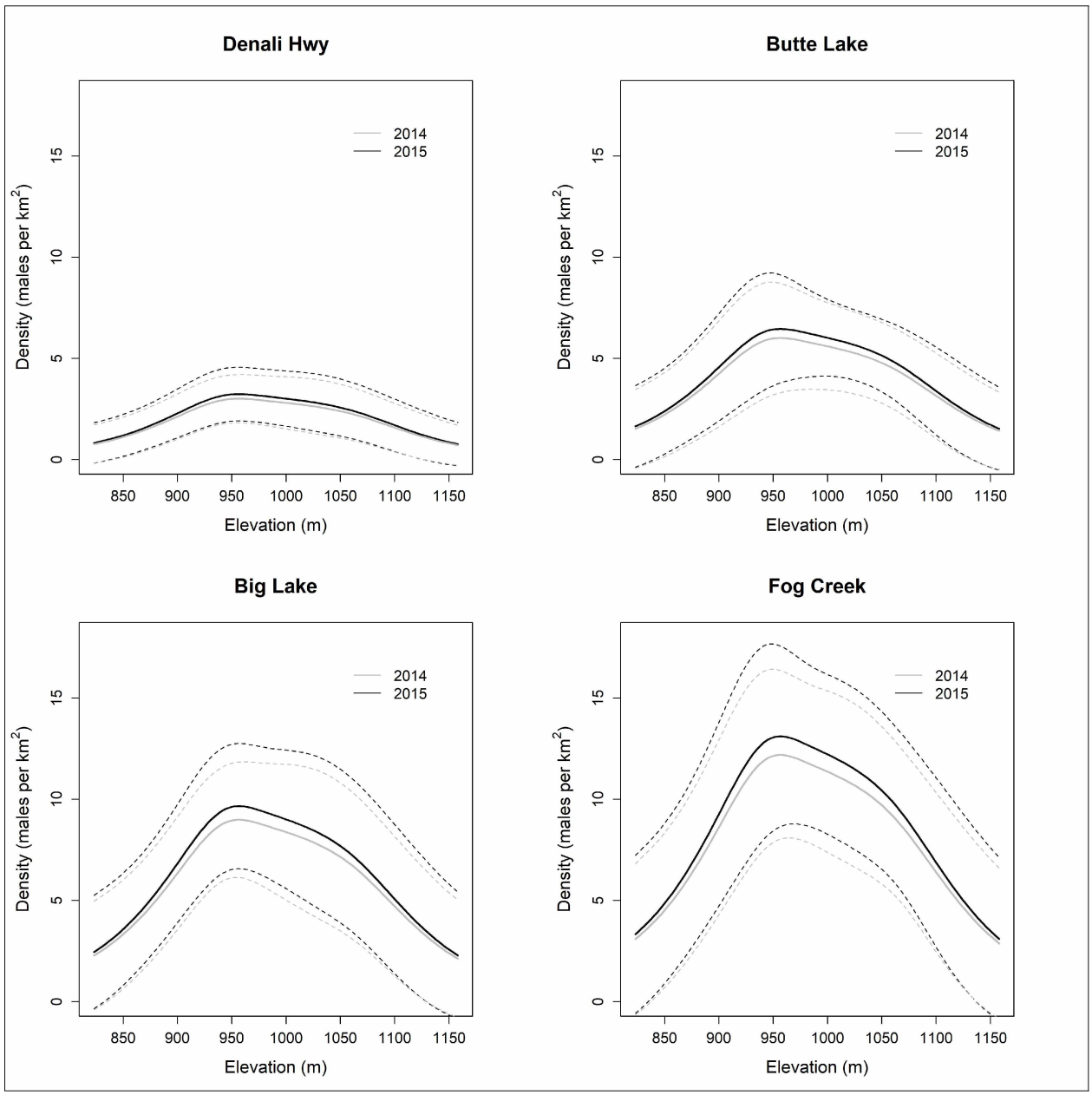

Figure 3.5: Estimated relationship between elevation and density of willow ptarmigan (*Lagopus lagopus*) breeding territories in southern Interior Alaska, USA.

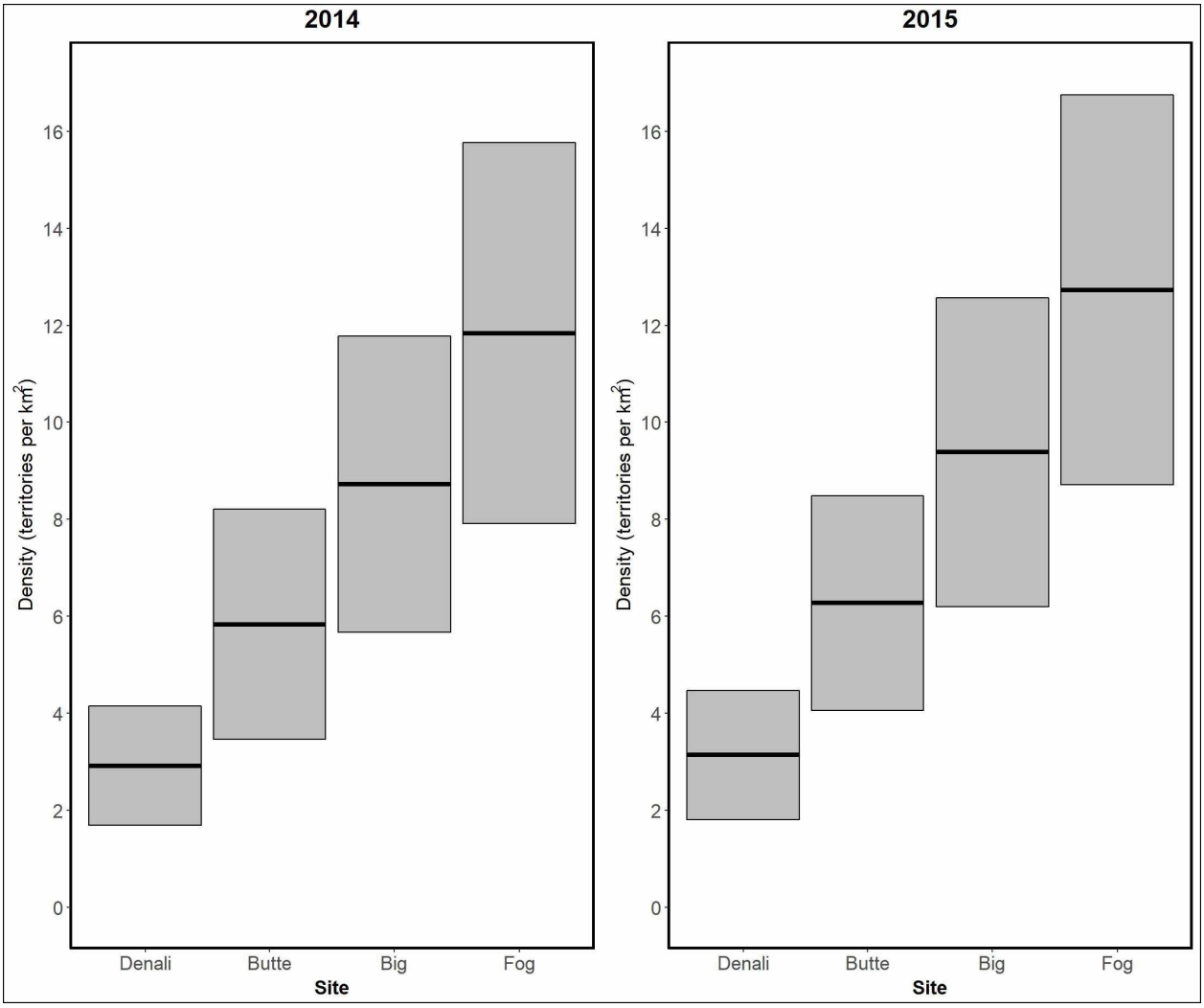

Figure 3.6: Predicted willow ptarmigan (*Lagopus lagopus*) density estimates while holding elevation and distance to lake/stream constant at their median values (980 m and 256 m, respectively). Black lines are point estimates and shaded boxes represent 95% confidence intervals.

3.10 Tables

Table 3.1: Estimates of willow ptarmigan (*Lagopus lagopus*) breeding territory abundance, 95% confidence intervals (95% CI), coefficient of variation (CV; standard error divided by the point estimate), area, and density estimate for each of four study sites during two years in southern Interior Alaska, USA.

Site	Year	Abundance[a]	95% CI	CV	Area (km^2)	Density[b]
Denali Hwy	2014	73	48-112	0.22	40.4	1.8
Butte Lake	2014	278	186-416	0.20	82.7	3.4
Big Lake	2014	609	440-844	0.17	114.6	5.3
Fog Creek	2014	436	300-634	0.19	82.6	5.3
Denali Hwy	2015	80	52-122	0.21	40.4	2.0
Butte Lake	2015	303	215-428	0.17	82.7	3.7
Big Lake	2015	665	487-907	0.16	114.6	5.8
Fog Cr	2015	476	332-683	0.19	82.6	5.8

Table 3.2: Parameter estimates from a model of willow ptarmigan (*Lagopus lagopus*) density as a function of site, year, and habitat-proxy covariates. The covariate corresponding to the estimated parameters is in parentheses. A Tweedie response distribution with exponential parameter p = 1.1 and a log link function were used to fit the model.

Parametric coefficients	Estimate	SE[a]	*t*-statistic	*P*-value
β_0 (intercept[b])	-12.92	0.19	-69.769	<0.001
β_1 (2015)	0.06	0.17	0.347	0.73
β_2 (Butte Lake)	0.67	0.28	2.45	0.02
β_3 (Big Lake)	1.05	0.23	4.56	<0.001
β_4 (Fog Lakes)	1.37	0.30	4.631	<0.001

Smooth terms	EDF[c]	*F*-statistic[d]	*P*-value[e]
Elevation	3.59	2.44	0.04
Distance to water	1.1	14.17	<0.001

Chapter 4: Potential Effects of Seasonal Movements and Dispersal on Compensation in a Hunted Willow Ptarmigan Population[3]

4.1 Abstract

Demographic compensation is a fundamental concept in harvest research and management. Forms of compensation vary among populations and harvest regimes, with a variety of factors determining the efficacy of different mechanisms. Research emphasis is most often placed on compensatory mortality; however, other mechanisms may facilitate compensation for harvest mortality and, in some populations, may have greater compensatory potential than density-dependent decreases in natural mortality. Although less frequently considered, immigration is often a viable compensatory mechanism for mobile species. Assessing the potential for compensatory immigration requires a population-specific understanding of movement ecology. We studied the movement ecology of a population of willow ptarmigan (*Lagopus lagopus*) with spatially heterogeneous hunting pressure in southern Interior Alaska, USA. Seasonal movements away from breeding territories were larger for adult females than for adult males, with maximum monthly median distances from territories of 48.0 km and 5.0 km, respectively. Elevations of wintering locations averaged slightly lower than breeding territories for all demographic groups, but variation within months was large. Breeding site fidelity was high, but females exhibited more variation in breeding dispersal distances (range: 0.12-6.31 km) than males (range: 0.07-1.44 km). Natal dispersal distances were more varied (range: 0.47-12.51 km), but sample sizes were limited due to high mortality rates between breeding seasons. Seasonal movements away from breeding territories occurred after the hunting season had begun, whereas movements back to the vicinity of territories occurred after the end of the hunting season in spring, resulting in greater vulnerability of local breeders to harvest during the early hunting season. After movements away from territories were initiated, movement magnitudes were large enough to result in the spatial mixing of ptarmi-

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gan from hunted and unhunted breeding areas during the remainder of the hunting season; thus harvest in hunted areas was no longer solely concentrated on local breeders. Breeding and natal dispersal distances suggested that potential for compensation via dispersal may be limited to hunted areas that are relatively small.

4.2 Introduction

Demographic compensation is a fundamental concept in harvest management. Compensation for harvest can occur via several possible mechanisms, including changes in natural mortality (e.g., Anderson and Burnham 1976, Roseberry and Klimstra 1984, Bartmann et al. 1992), natality (Gaillard et al. 1998, Myrberget 1984, Swenson 1985, Bro et al. 2003), or immigration (Pulliam 1988, Smith and Willebrand 1999, Martin et al. 2000). Although compensation is a nearly ubiquitous topic in harvest research, many studies do not investigate compensatory mechanisms, but rather the numeric response of populations to harvest (e.g., Bergerud and Huxter 1969, McGowan 1975, Pedersen et al. 2004). When compensatory mechanisms are studied, emphasis is most often placed on compensatory mortality (e.g., Burnham and Anderson 1984, White and Bartmann 1998, Sandercock et al. 2011). However, other mechanisms may facilitate compensation for harvest mortality and, in some populations, may have greater compensatory potential than density-dependent decreases in natural mortality (Johnson et al. 1986, Lebreton 2005, Lindberg et al. 2013, Caudill et al. 2017). Although less frequently considered than mortality, immigration is often a viable compensatory mechanism and has been documented for several mobile species (e.g., cougar, *Puma concolor*, Robinson et al. 2008; eagle owl, *Bubo bubo*, Schaub et al. 2010; wolverine, *Gulo gulo*, Gervasi et al. 2015). For territorial species with annual birth pulses, compensation for harvest mortality via immigration could occur through breeding dispersal, natal dispersal, or both (*sensu* Greenwood 1980). The potential for immigration to compensate for harvest depends on the specific characteristics of individual populations. In particular, dispersal distances and rates must be sufficient to enable individuals to occupy areas vacated

by harvested individuals, and immigration in harvested populations must be greater than emigration so as to function as a harvest-induced source-sink system.

In addition to permanent immigration via breeding dispersal (movement from one breeding location to subsequent breeding location) or natal dispersal (movement from natal site to first breeding location), seasonal movements (temporary movements between breeding seasons) have the potential to influence the role of harvest in population dynamics. The effects of harvest on local breeders may be mitigated by seasonal movements because both hunting seasons and seasonal movements away from territories typically occur outside of the breeding season. For populations that exhibit seasonal movements in landscapes with heterogeneous hunting pressure, these movements to and from breeding sites may thus dampen the impact of harvest. This could occur through breeders from unhunted breeding populations using hunted areas outside of the breeding season and absorbing some portion of the seasonal hunting mortality in those areas. Conversely, it could occur when breeders from hunted breeding populations seasonally move out of hunted breeding areas into refugia without hunting, thereby reducing their potential harvest exposure. The timing of hunting seasons (Boyce et al. 1999, Kokko 2001, Caudill et al. 2014, Blomberg 2015, Caudill et al. 2017), size of hunted areas (Pulliam 1988, Brseth et al. 2005, Hörnell-Willebrand et al. 2014), and magnitude of harvest all affect the way seasonal movements impact local breeding populations. To evaluate the potential role of immigration and seasonal movements in the dynamics of harvested populations, a population-specific understanding of movement ecology is required.

Seasonal movements are typically not homogeneous within species. Rather, differential seasonal movements between sexes are common in vertebrates (e.g., Lack 1968, Ketterson and Nolan 1983, Alerstam and Hedenström 1998, Alerstam et al. 2003). Similarly, both breeding and natal dispersal often differ between the sexes (Greenwood and Harvey 1982). Typically, females make larger seasonal and dispersal movements in avian species, whereas males do so in mammalian species (Greenwood 1980); however, exceptions to this pattern

exist in several taxa (e.g., waterfowl, Clarke et al. 1997, Wolff and Plissner 1998; banner-tailed kangaroo rat, *Dipodomys spectabilis*, Mabry et al. 2013). In ptarmigan (*Lagopus spp.*), as in other tetraonids, females typically disperse farther than males (Johnsgard 1983, Martin and Hannon 1987, Giesen and Braun 1993, Martin et al. 2000, Schiek and Hannon 1989). Previous studies have indicated that female ptarmigan move farther from breeding territories than males during winter, but the magnitudes of reported sexual differences have varied among regions (Weeden 1964, Irving et al. 1967, Gruys 1993, Hörnell-Willebrand et al. 2014). Sexual segregation appears to be common for ptarmigan during this period (Weeden 1964, Irving et al. 1967, Mossop 1988, Gruys 1993) and some authors have suggested that females in North America move to lower elevations in winter than males (Weeden 1964, Gruys 1993). However, to our knowledge, this hypothesis has not been rigorously examined.

Ptarmigan (*Lagopus* spp.) are among the most popular small game species in Alaska, USA, composing approximately 54% of the statewide annual upland game bird harvest, with willow ptarmigan (*Lagopus lagopus*) accounting for the majority of the harvest (Merizon et al. 2014). However, the magnitude of willow ptarmigan harvest varies dramatically among regions in Alaska, largely because of limited access to most areas of the state. This has resulted in an association between heavy harvest and access corridors. Detailed information on the impact and sustainability of concentrated ptarmigan hunting within access corridors is limited; however, recent estimates have suggested low breeding densities of willow ptarmigan in these corridors (Chapter 3). An important step in managing ptarmigan harvest is assessing the potential role of different compensatory mechanisms in ptarmigan population dynamics.

Our objective was to describe the seasonal movements and dispersal patterns of willow ptarmigan in southern Interior Alaska and to address several related hypotheses. First, we examined the hypothesis that seasonal movements dampen the effect of harvest on ptarmigan breeding in hunted areas. Second, we postulated that females exhibit seasonal movements of greater magnitude than males. Third, we hypothesized that females move to lower elevations than males during winter. Finally, we examined the hypotheses that breeding dispersal and

natal dispersal are of sufficient magnitude to compensate for harvest in adjacent populations. An understanding of these aspects of willow ptarmigan movement ecology will help to elucidate the extent to which different compensatory mechanisms influence the dynamics of hunted populations.

4.3 Study Area

We conducted this study in the southern Alaska Range and northern Talkeetna Mountains in southern Interior Alaska, USA (Figure ??). Within this region, we designated five study sites, with varied accessibility. Two sites were accessible by highway vehicle, whereas three sites were accessible primarily by small aircraft. Sites were similar in terms of habitat characteristics but differed in the degree of use for hunting and other recreational activities. The accessible study sites received substantial use, including hunting, as well as non-consumptive forms of recreation (e.g., hiking, all-terrain vehicle use, snowmobile use). In contrast, human use of the remote sites was extremely limited. The ptarmigan hunting season began 10 August and continued through 31 March during the years of this study.

Elevations at the study sites ranged from 850-1,230 m. These sites contained a mix of un-vegetated rocky slopes, open tundra-dominated hills, shrub tundra, and riparian areas. Shrub species were primarily dwarf birch (*Betula nana*, *B. glandulosa*), alder (*Alnus* spp.), and willow (*Salix* spp.). Lower elevations were characterized by subalpine spruce (*Picea* spp.) stands and taller stands of dwarf birch.

4.4 Methods

4.4.1 Field Methods

We deployed very high frequency (VHF) radio-transmitters on ptarmigan from 2013-2015. We captured adults during April, May, and August and juveniles ($\backsim$60-80 days old) during August. We located territorial ptarmigan using a combination of visual scanning and broadcasted recordings of conspecific vocalizations to elicit vocal responses. After locating

ptarmigan, we lured individuals to capture equipment using conspecific decoys and recordings of conspecific vocalizations. We captured ptarmigan using: (1) mist nets erected in flight lanes, (2) gill nets strung around vegetation, through which ptarmigan travelled on foot, (3) net guns to capture birds both in the air and on the ground, (4) noose carpets constructed with monofilament snares to capture birds that approached decoys closely, and (5) bow nets to capture birds that approached decoys closely. Upon capture, ptarmigan were fitted with 12 g VHF transmitters (Advanced Telemetry Systems, Isanti, MN, USA), using necklace-style harnesses (Amstrup 1980). Transmitters weighed $< 3\%$ of body weight for all radio-collared individuals. Each transmitter contained a mortality switch, which increased the pulse rate of VHF signals after 10 hrs of inactivity.

We located radio-marked ptarmigan approximately monthly from June 2013 through June 2016 using small fixed-wing aircraft. During aerial telemetry flights, we recorded the location of radio-marked birds using Global Positioning System (GPS) receivers. To estimate distances and altitudinal changes of seasonal movements, we used capture locations in May to represent the location of breeding and natal territories. For adults and juveniles that were initially captured in August, we used the May location of the previously radio-collared adult with which they were associated to represent the locations of breeding and natal territories, respectively. These were reasonable approximations of territory locations, as breeding pairs have established territories in May in our study area.

We computed geodesic distances from breeding (adults) and natal (juveniles) territories to ptarmigan locations during each month and the subsequent breeding season (May). We used locations during the subsequent breeding season to estimate breeding and natal dispersal for adults and juveniles, respectively. Distributions of seasonal distances were partitioned by demographic group (adult male, adult female, juvenile). We considered juveniles as a single group because of the uncertainty of sex assignment during the first months of life when they were captured (Pyle 2008).

4.4.2 Data Analysis

To address the hypothesis that seasonal movements have the potential to dampen the effects of harvest on local breeders, we modelled movement distance as a function of month, with month treated as a smoothed continuous term using penalized regression splines (Wood 2006). To flexibly describe movement patterns, we used a generalized additive mixed model (GAMM) with a gamma response distribution and optimized the smoothing parameter via generalized cross-validation (Wood 2006). We treated individual identity as a Gaussian distributed random intercept and included sex as a binary covariate on the mean parameter (μ) using a log link function to address the hypothesis that female movements are of greater magnitude than those of males. The model was parameterized as

$$Y \backsim \text{Gamma}(\mu, \alpha)$$

$$\text{Gamma}(\mu, \alpha) = \frac{1}{\Gamma(\alpha)} \left(\frac{\alpha y}{\mu} \right)^{\alpha} e^{-\frac{\alpha y}{\mu}} \frac{1}{y}$$

$$\log(\boldsymbol{\mu}) = X\boldsymbol{\beta} + \gamma$$

where Y is the random variable of interest, α is the gamma scale parameter, β is a vector of coefficients for the corresponding covariates in the design matrix, X, Γ denotes the gamma function, and γ is a Gaussian distributed random intercept.

Similarly, to address the hypothesis that females travel to lower elevations than males outside of the breeding season, we modelled change in elevation as a function of sex and a smoothed function of month. We calculated elevational changes relative to breeding season elevations. We used a GAMM with a Gaussian error distribution and again treated individual identity as a Gaussian distributed random intercept:

$$Y \backsim \text{Gaussian}(\mu, \sigma^2)$$

$$\boldsymbol{\mu} = X\boldsymbol{\beta} + \gamma$$

where Y is the random variable of interest, μ is the Gaussian mean parameter, σ^2 is the Gaussian variance parameter, β is a vector of coefficients for the corresponding covariates in the design matrix, X, and γ is a Gaussian distributed random intercept.

To examine the extent to which natal and breeding dispersal may be capable of compensating for harvest mortality, we described the observed distributions of natal and breeding dispersal distances for each demographic group (adult males, adult females, juveniles). We did not formally model dispersal distances because of limited samples sizes of dispersal measurements for juveniles and adult females.

We conducted all analyses in the R software environment (R Core Team 2018). We implemented GAMMs in the package mgcv (Wood 2018). We based inference on approximate P-values associated with the semi-parametric models (Wood 2006), as well as graphical comparisons of confidence intervals for predicted values.

4.5 Results

We deployed necklace-mounted VHF radio-transmitters on 243 willow ptarmigan between April 2013 and August 2015. The radio-marked sample was composed of 113 adult males, 62 adult females, and 68 juveniles. Seasonal movements differed substantially in magnitude among seasons ($F = 46.23$, $P < 0.001$) and demographic groups ($\hat{\beta} = 4.44$, $P < 0.001$; Figures ?? and ??). Adult female movements were highly variable and were the longest documented during the study. Adult male movements varied as well, but a greater proportion of males than females remained near breeding territories throughout the year. The magnitude of juvenile movements was intermediate relative to adult males and females (Figures ?? and ??). A seasonal pattern was evident in the data, wherein ptarmigan were distributed across a wide range of distances from breeding territories during the winter months, but largely returned to the vicinity of breeding territories during the subsequent breeding season (Figures ?? and ??). The timing of movements towards and away from breeding and natal territories was similar for all groups (Figures ?? and ??).

Although movement distances varied substantially, ptarmigan remained within a well-defined elevational band during all seasons. Ninety-five percent of locations occurred between 764 m and 1,277 m in elevation, with a median of 1,008 m. The predicted values from the fitted model and associated confidence intervals indicated a subtle seasonal pattern, with slightly higher average elevations used in late summer and slightly lower average elevations used during winter relative to adult breeding locations (Figures 4.4 and ??). Juveniles also used slightly lower elevations on average during winter relative to natal locations (Figures 4.4 and ??). However, the variation within demographic groups was large relative to seasonal differences (Figures 4.4 and ??). Adult females used slightly lower elevations than males during winter, but the magnitudes of the differences were small (Figure 4.4).

The median breeding dispersal distance of adult males was 0.27 km (range: 0.07-1.44 km), whereas the median distance for females was 0.73 km (range: 0.12-6.31 km; Fig. 6). The median natal dispersal distance was 5.43 km (range: 0.47-12.51 km; Fig. 6). Because of high annual mortality of females and juveniles in our study, the numbers of adult females that survived to a subsequent breeding season and juveniles that survived to their first breeding season were small (n = 13 and n = 11, respectively) relative to adult males (n = 33).

4.6 Discussion

Our results suggest that immigration via breeding dispersal is an unlikely compensatory mechanism for willow ptarmigan in our study area because of limited breeding dispersal distances and corresponding high breeding site fidelity. Natal dispersal appears to be a more plausible mechanism because the distances moved by juveniles to their first breeding sites were greater than those of adults. However, for natal dispersal to effectively compensate for harvest, harvested areas would need to be small enough that juveniles from adjacent refugia could enter during dispersal. In addition, seasonal movements may help to dampen the effects of harvest by spatially mixing individuals from hunted breeding sites with those from unhunted refugia during much of the hunting season. The fact that females exhibit

larger movements than males (Figures ?? and ??)—and thus are more spatially mixed than males during the non-breeding seasons—may aid in ameliorating the effects of harvest in accessible areas because female survival was a sensitive vital rate in this population.

The shorter average movement distances we observed for males were consistent with our hypotheses, with evidence for stronger breeding site fidelity in males (Figures ?? and ??). Juvenile seasonal movements were similar to those of adult males and females; however, as in previous studies (Myrberget 1976, Martin and Hannon 1987, Brøseth et al. 2005, Hörnell-Willebrand et al. 2014), average natal dispersal distances were larger, with greater variation, than adult breeding dispersal distances of either sex (Figures ??). There was a subtle trend in the use of lower elevations during winter for all demographic groups, but individual variation within demographic groups and months was relatively large (Figures 4.4 and ??). The slightly lower elevations used by adult females relative to males during winter were consistent with the differential elevation hypothesis, but the magnitude of the difference was small (Figure 4.4).

Seasonal locations of willow ptarmigan revealed a clear temporal pattern of movements, with birds remaining close to breeding/natal territories during the breeding and brood-rearing season but distributing widely after the breeding season until the following breeding season (Figures ?? and ??). The magnitude, frequency, and duration of seasonal movements outside of the breeding season were great enough that spatial mixing of individuals from breeding areas with and without hunting could occur. The hunting season for ptarmigan in our study area began in August, prior to most movement away from territories, and ended in March, which was shortly before most ptarmigan returned to the vicinity of the previous years territories (Figures 4.4 and ??). Thus, early-season harvest (prior to seasonal movements away from breeding territories) could potentially have a greater direct impact on local breeders. This is consistent with results from a concurrent study of willow ptarmigan survival in our study area (Chapter 2). During that study, survival rates were lower for birds breeding at hunted sites than those breeding at non-hunted sites during the early hunting

season, but survival did not differ between the groups after greater seasonal movements were initiated. Interestingly, this is contrary to the paradigm in which late-season harvest is viewed as having the greatest impact because of reduced potential for compensatory survival (Kokko and Lindström 1998, Kokko 2001, Ratikainen et al. 2008, Blomberg 2015). Although late-season harvest may be a more additive form of harvest mortality, seasonal movement patterns may negate the impact of late-season harvest if seasonal migrants have not yet returned to breeding territories when hunting seasons close, especially in regions that experience spatially heterogeneous harvest. Seasonal movements to and from areas with varied hunting pressure play a role in the harvest dynamics of other tetraonid species as well, including greater sage-grouse (*Centrocercus urophasianus*, Caudill 2014, 2016), and dusky grouse (*Dendragapus obscurus*, Mussehl 1960). Annual variation in the timing of these seasonal movements can influence the success of huntersand thus the magnitude of harvestin some tetraonid populations (e,g., dusky grouse, Mussehl 1960; greater sage-grouse, Caudill et al. 2014, 2016). However, this effect depends on both the timing of seasonal movements and the timing of hunting seasons. In our study area, the hunting season began on 10 August and was well underway prior to the initiation of large seasonal movements by ptarmigan, making it unlikely that annual variation in the timing of movements would alone cause substantial changes in annual harvest.

The larger seasonal movements of adult females relative to adult males (Figure **??**) suggest that the former has greater potential to dampen the effects of harvest on local breeding populations in hunted areas when harvest is localized. The largest monthly median distance of males from breeding territories was 5.0 km, whereas the largest monthly median distance of females from breeding territories was 48.0 km (Figure **??**). These differential movement patterns are consistent with previous studies of willow ptarmigan movements (Weeden 1964, Bergerud and Gratson 1988, Gruys 1993, Hörnell-Willbrand et al. 2014). However, the magnitudes of movements in our study were greater than those reported for willow ptarmigan in Europe (e.g., Hörnell-Willbrand et al. 2014). A variety of hypotheses have been

advanced to explain differential movements of the sexes in birds, including the body-size hypothesis, which states that larger bodied individuals are better suited to withstand colder winter conditions at higher latitudes and elevations (Ketterson and Nolan 1983). Although the latitudinal aspect of this hypothesis is likely not relevant to ptarmigan (however, see Irving et al. 1967 and Christie et al. 2014 for description of apparent latitudinal migrations in arctic ptarmigan), this could explain movements to lower elevations by females. Another hypothesis states that males remain close to territories, so that they can easily return and defend them against conspecifics during the subsequent breeding season, whereas females move as far as necessary to maximize access to resources during winter (Myers 1981, Bergerud and Gratson 1988, Kettering and Nolan 1983, Gruys 1993, Schwab et al. 2005). The social-dominance hypothesis (Gauthreaux 1978, 1982, Ketterson and Nolan 1983) states that socially dominant individuals (males in the case of ptarmigan) displace subordinate individuals, resulting in segregation of the sexes and differential seasonal movements. All of these hypotheses provide plausible explanations for the movement patterns we observed, but we cannot distinguish among them on the basis our data.

In addition to greater seasonal movement distances, previous investigators have hypothesized that female willow ptarmigan move to lower elevations than do males during the winter (Weeden 1964, Irving 1967, Gruys 1993). Our results suggest that females did move to slightly lower elevations relative to breeding locations than did males on average, but the magnitude of the difference was small enough that we question whether it was ecologically important (Figures 4.4). Similarly, although locations during mid-late winter averaged slightly lower in elevation than breeding/natal locations for all demographic groups, the magnitude of the difference was small relative to the observed monthly variation in elevation (Figures 4.4 and **??**). Average elevations for both sexes of adults were slightly higher during the brood rearing period (Figures 4.4 and **??**); however, as in the winter, the magnitude of the difference was small relative to individual variation. Nevertheless, previous investigators have also noted uphill movements by ptarmigan broods (Gelting 1937, Gardarsson and Moss

1970, Andersen et al. 1986, Gruys 1993, Merizon et al. 2018). Andersen (1986) suggested that variation in the extent of uphill movements was a function of snowmelt timing, which is related to plant phenology. Although this is a plausible hypothesis, we did not collect snowmelt or plant phenology data with which to evaluate it. The elevation range within which willow ptarmigan remained throughout the year (95% of locations between 764 m and 1277 m) corresponded primarily to the shrub-tundra habitats with which they are typically associated (Viereck et al. 1992). The intermediate distribution of juvenile distances and elevations during most seasons may have resulted from our inability to differentiate between sexes. Each juvenile sex may have exhibited movements similar to adults of the same sex, resulting in a blended distribution when pooled. Previous observations have suggested that juveniles of both sexes primarily aggregate with flocks of adult females during their first winter (Weeden 1964, Irving 1967, Höhn 1984), but the intermediate distribution of juvenile movements we observed suggests that this may not be the case in our study area. For all demographic groups, seasonal elevation changes were small enough that it is uncertain how ecologically significant they were.

As with seasonal movements, adult females exhibited a greater range of breeding dispersal distances than did adult males (Figure ??). This is consistent with previous willow ptarmigan research in suggesting high breeding site-fidelity for adult males and moderate site-fidelity for adult females (Schieck and Hannon 1989, Hörnell-Willebrand 2014). As with seasonal movement distances, the range of natal dispersal distances observed was likely a partial consequence of not distinguishing between male and female juveniles. Most previous research has suggested greater natal dispersal distances for females than males, as is typical in tetraonids (Martin and Hannon 1987, Hörnell-Willebrand et al. 2014). Sex-biased dispersal has implications for the effectiveness of compensatory immigration because it can limit the composition of immigrants to only or primarily one sex. For example, Oliver et al. (2016) concluded that male-biased dispersal in mink reduced the potential for compensation because immigrants were male and thus could not effectively establish new breeding pairs.

Because female-biased dispersal appears to be most common in ptarmigan and polygyny increases in frequency when sex-ratios are unbalanced in favor of females (thereby allowing reproduction by immigrants; Hannon 1984), dispersal may still be an effective means of compensating for ptarmigan harvest at scales that are small enough to allow dispersal between areas with and without harvest. It is important to emphasize, however, that our sample of juveniles that survived to establish a breeding territory was small, as was our sample of adult females that survived to a subsequent breeding season.

The potential for seasonal movements and dispersal to moderate the effects of harvest depends in part upon the size of areas in which harvest is concentrated (Pulliam 1988, McCullough 1996, Schaub et al. 2010, Hörnell-Willebrand et al. 2014). If concentrated harvest occurs in areas that are small relative to dispersal distances, compensatory immigration is more likely to occur. In contrast, if harvested areas are large relative to dispersal distances, compensatory immigration is unlikely to occur. Seasonal movements and dispersal may be of greater benefit to females because of differential movements between the sexes, which is significant because female survival is a more sensitive vital rate than male survival. Observed breeding dispersal distances in our study suggest that immigration from adjacent populations via breeding dispersal has limited potential to compensate for harvest in heavily hunted access corridors, especially for adult males (Figure ??). Natal dispersal from adjacent populations without hunting may have the potential to compensate to a greater degree if hunted areas are relatively small (Figure ??). However, these conclusions are highly dependent upon the size and configuration of areas that are heavily hunted (Hörnell-Willebrand 2014). Our sampling design was insufficient for quantifying the spatial extent of concentrated harvest. In companion studies to the present one, we found that differences in abundance and survival existed between sites with and without hunting (Chapters 2 and 3), but the exact spatial extent of areas affected by hunting in our study area is unknown.

Breeding densities at our study sites were inversely proportional to accessibility and hunting pressure (Chapter 3). However, because high mortality in our study populations limited

the number of birds that survived from one breeding season to the next, we were unable to address hypotheses of density-dependent dispersal by comparing dispersal of ptarmigan from hunted sites to dispersal of those from sites without hunting. Density dependence is a plausible condition for compensatory immigration, as territorial spacing may limit local breeding options when densities are high (Fretwell and Lucas 1969). However, ptarmigan populations fluctuate dramatically in most regions and data from a neighboring study suggest that we conducted this study during a low-density phase of these fluctuations (Schmidt et al. 2018). If dispersal rates and magnitudes are density dependent, then there may be greater potential for compensation via immigration when densities are higher. Such a situation could result in a greater disparity in breeding densities in adjacent populations with and without hunting, thereby increasing density-induced dispersal from higher-density, unhunted sites into lower-density, hunted sites. Thus, our results should be considered in the context of low-density population phases and may not accurately depict ptarmigan movement ecology at higher densities. Density-dependent dispersal of willow ptarmigan was inferred during one study in central Norway (Rørvik, Pedersen, and Steen 1998), but not during a later study in the same region (Brøseth et al. 2005). Brøseth et al. (2005) suggested that this discrepancy may have been related to the relative densities during the two studies, as the first study occurred when pre-harvest densities were > 50 birds per km^2, whereas the second study occurred when densities were < 30 birds per km^2.

Even in the absence of density-dependent dispersal rates, immigration could effectively compensate for harvest if densities are higher in unhunted refugia than in adjacent hunted areas. In that situation, dispersal rates and distances could be similar among hunted and unhunted areas, but a greater number of individuals would be dispersing from the higher density unhunted area than from the lower density hunted area, resulting in net immigration in the hunted areas. However, such a scenario would again be highly dependent on the size of hunted areas being small enough to allow exchange of individuals via dispersal (Pulliam 1988, McCullough 1996, Schaub et al. 2010, Hörnell-Willebrand et al. 2014). In addition

to movements influencing the impacts of hunting, there is potential for hunting disturbance to stimulate movements of ptarmigan out of hunted areas. However, Brøseth and Pedersen (2010) found no effect of hunting disturbance on emigration of ptarmigan in Fennoscandia.

Our results suggest that dispersal may have some limited potential to compensate for harvest if harvest is concentrated in relatively small areas, or in linear corridors with relatively small widths. In contrast, seasonal movements appear to be large and frequent enough that they have the potential to dampen the effects of harvest on local breeding populations with less of a constraint on the size of areas in which harvest is concentrated. This is consistent with survival estimates from a concurrent study (Chapter 2), which indicated that seasonal survival of ptarmigan prior to initiation of seasonal movements was substantially lower in accessible, hunted areas than in remote areas without hunting, resulting in lower annual survival in hunted areas because of a lack of seasonal compensatory mortality. Consequently, breeding densities were lower in the hunted, accessible areas as well (Chapter 3). Thus, timing hunting seasons to begin after seasonal movements are initiated in the fall may be an effective management tool in areas where overharvest of local breeders is of concern. Future research should emphasize differences in natal and breeding dispersal between areas with and without harvest. Due to high annual mortality (Chapter 2), our samples were too small to formally model dispersal as a function of hunting pressure or density. In addition, study designs that help to more rigorously define the size of areas in which harvest is concentrated would be valuable in allowing these results to be applied directly to harvest management.

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4.9 Figures

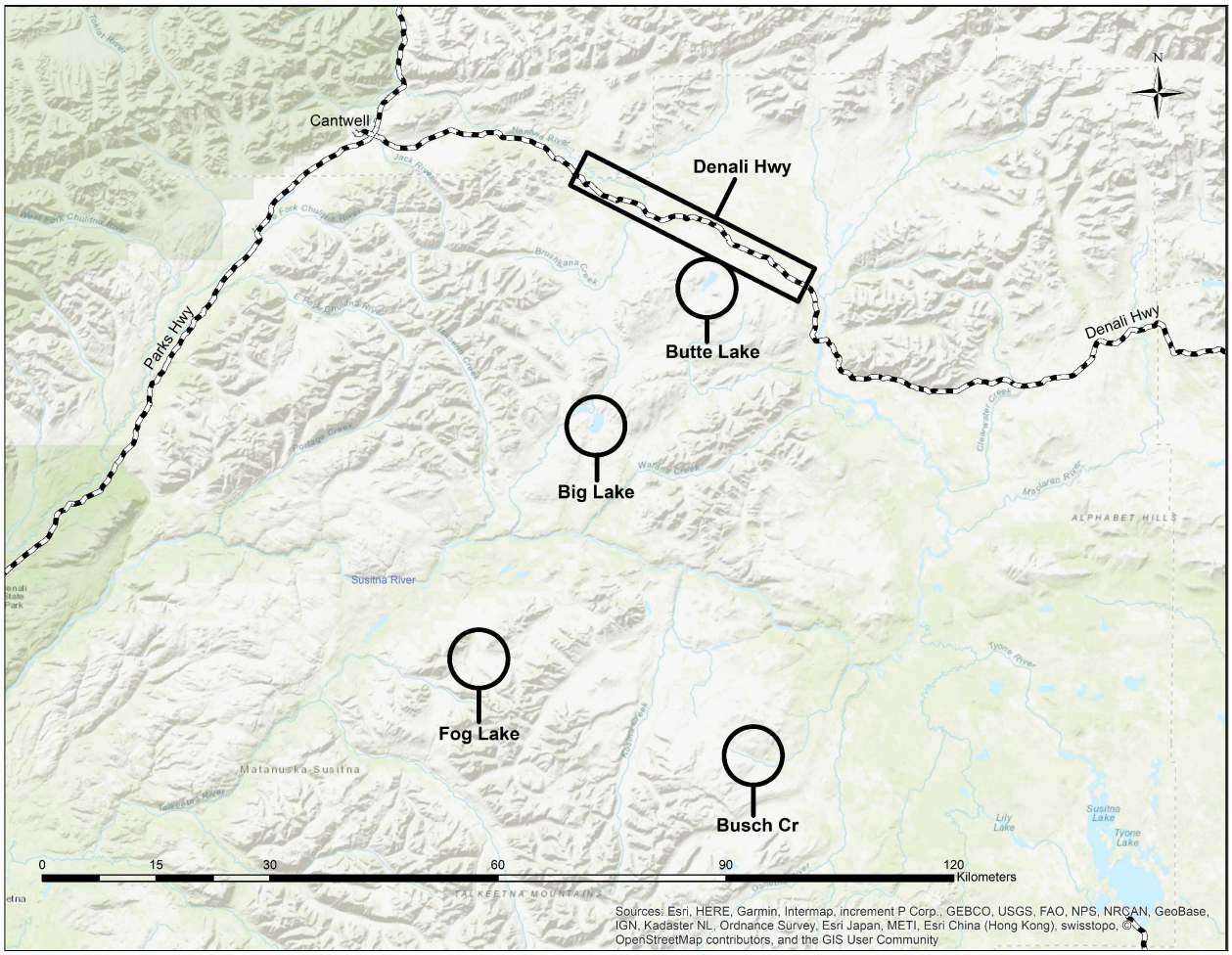

Figure 4.1: Willow ptarmigan (*Lagopus lagopus*) study sites in southern Interior Alaska, USA.

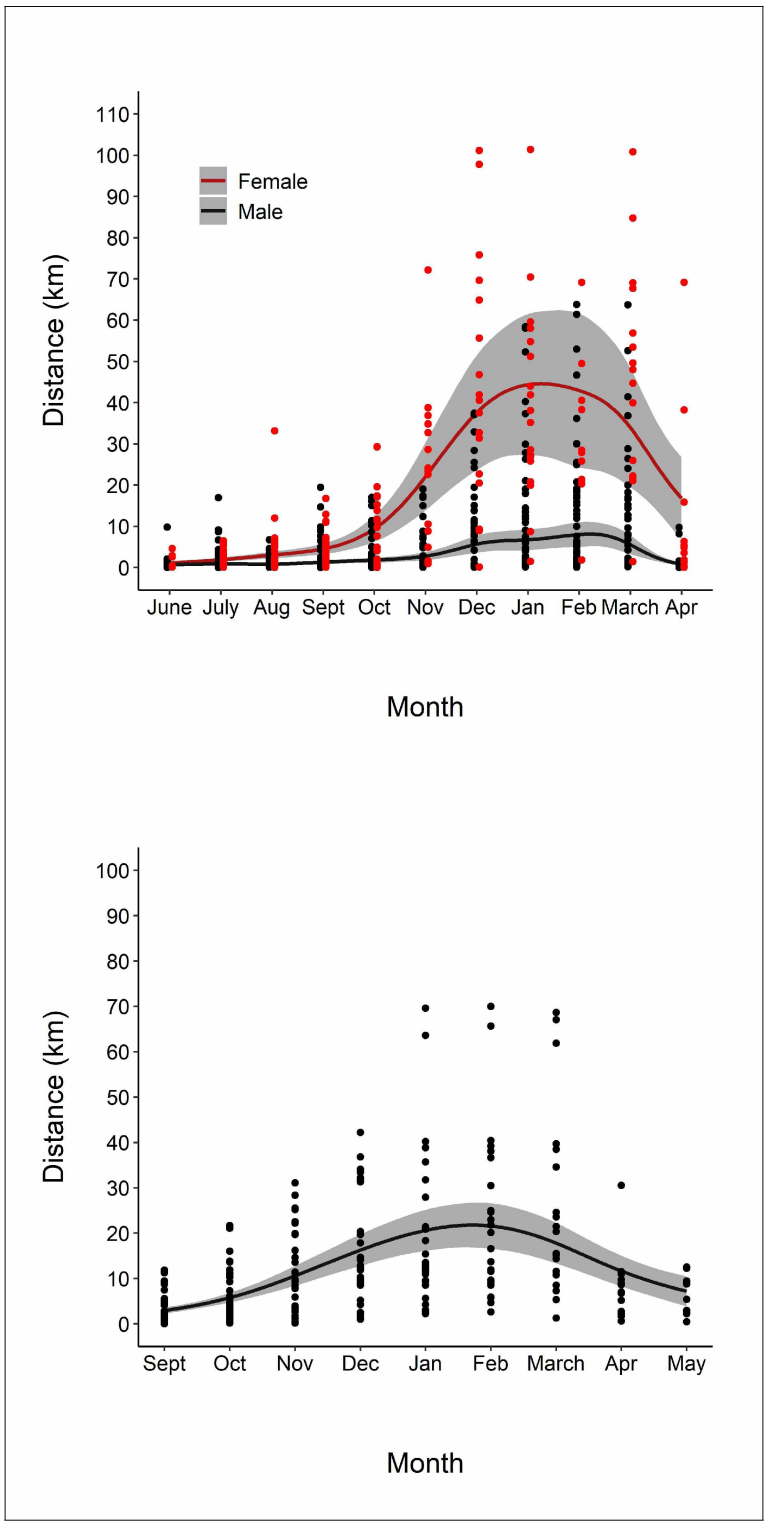

Figure 4.2: Smoothed trend in seasonal movement distance from breeding territory across months for adult male and adult female (top panel) and juvenile (bottom panel) willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA.

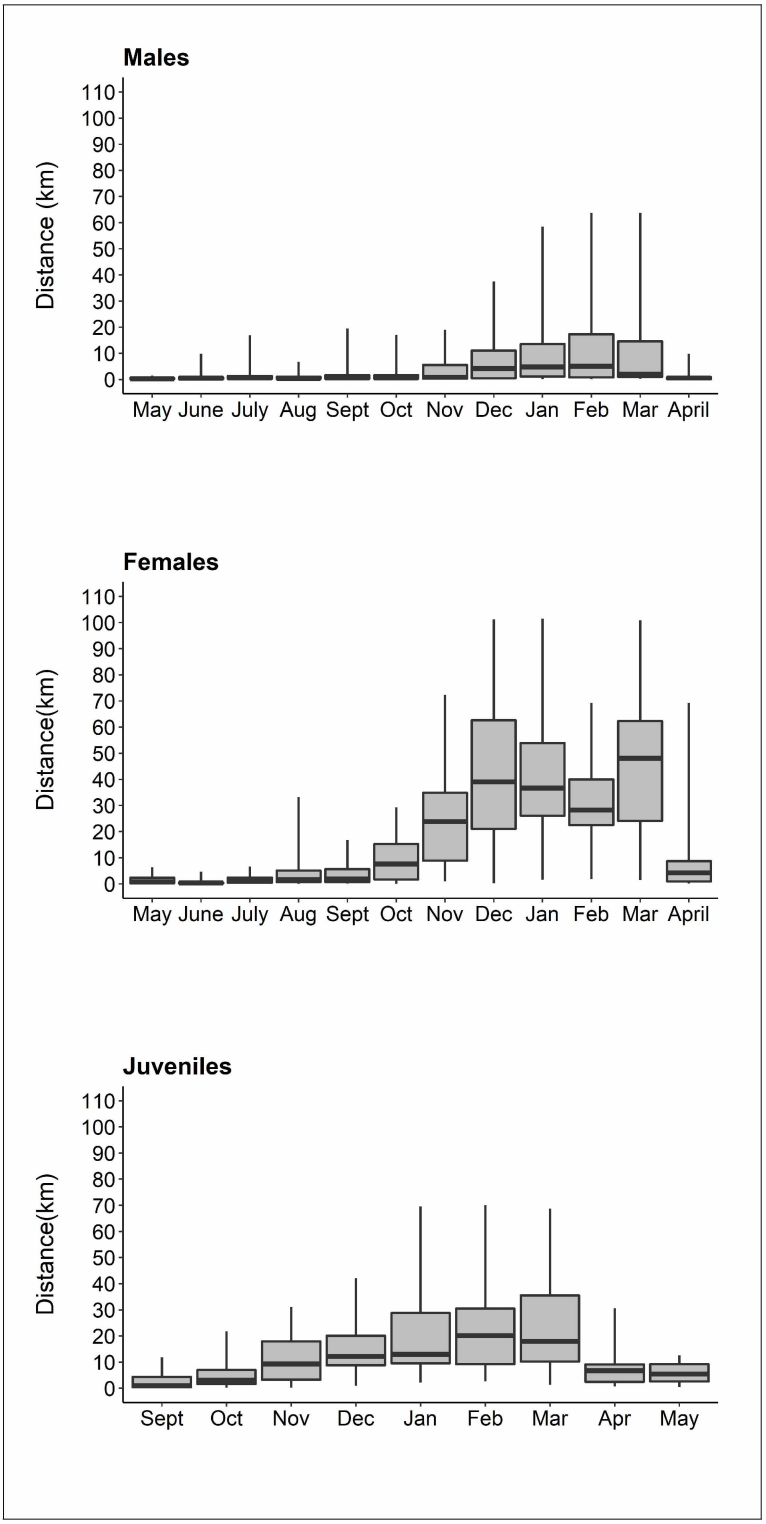

Figure 4.3: Monthly distributions of distances from breeding (adult male and female) and natal (juvenile) territories for willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA. The center horizontal lines depict median distances for each month, the gray box represents the interquartile range (the 0.25 quantile to the 0.75 quantile), and the vertical whiskers depict the range.

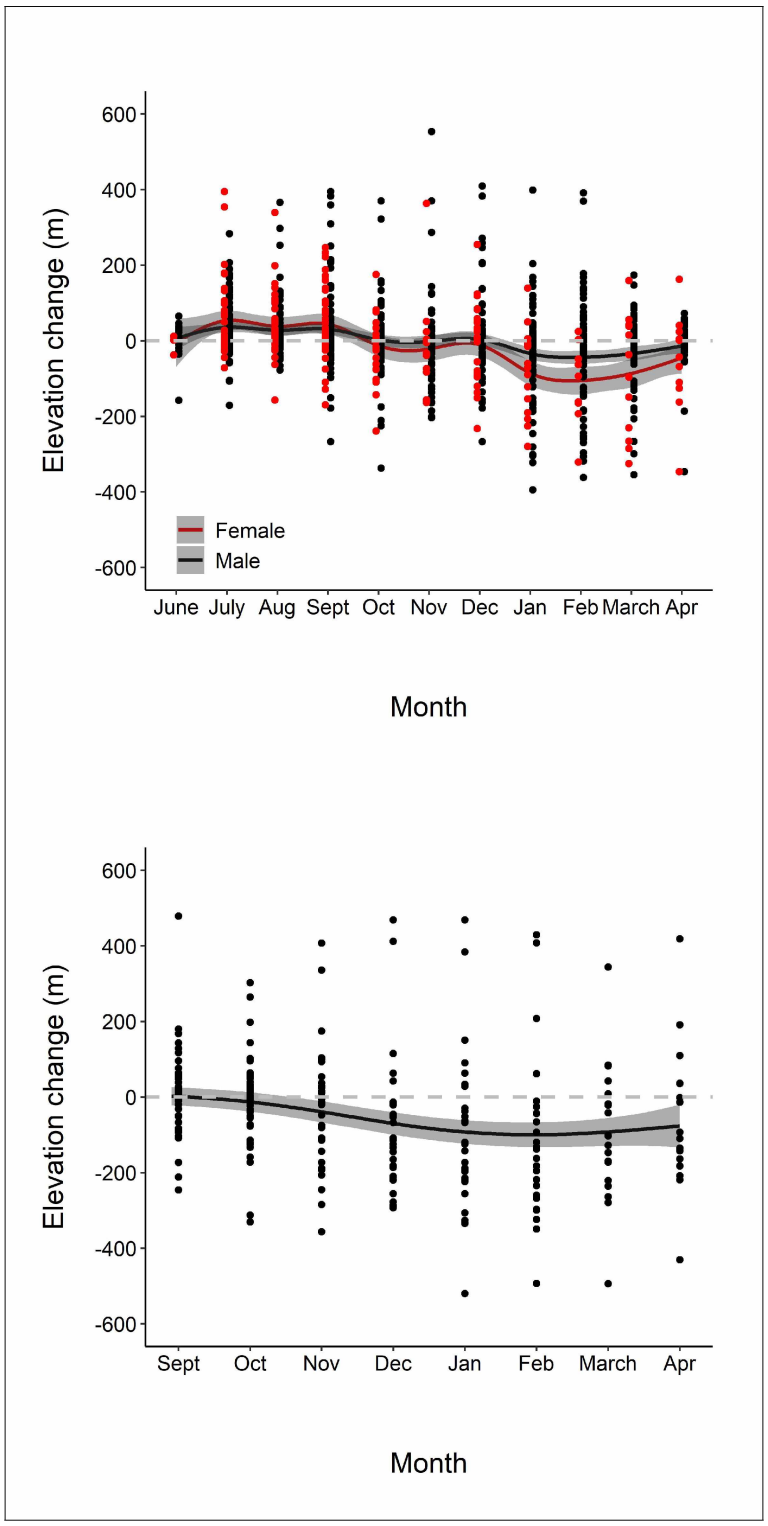

Figure 4.4: Smoothed trend in elevation use across months for adult male and female willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA. Elevation change was measured relative to the elevation of breeding territories.

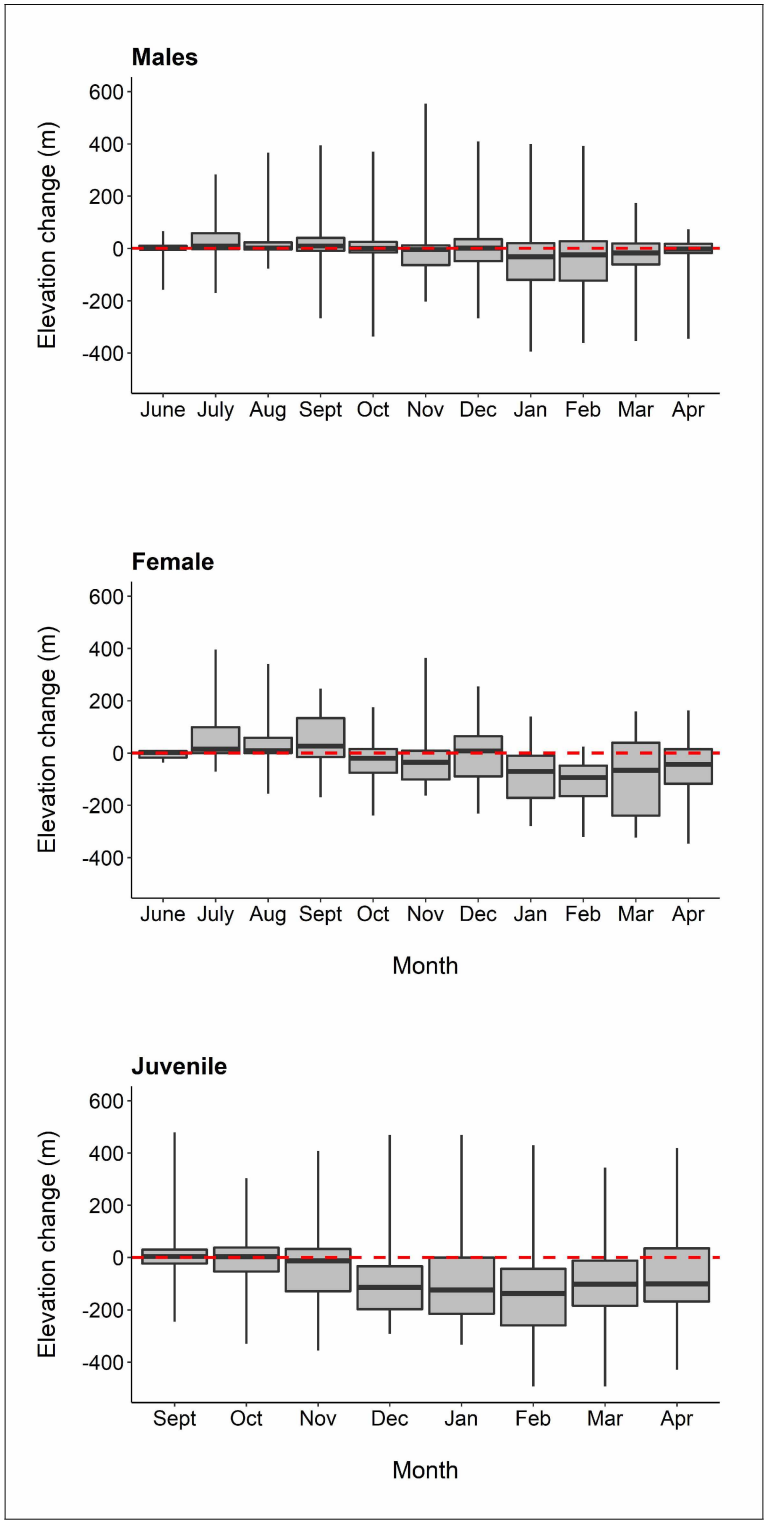

Figure 4.5: Monthly distributions of elevations relative to elevations of breeding (adult male and female) and natal (juvenile) territories for willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA. The center horizontal lines depict median elevation change for each month, the gray box represents the interquartile range (the 0.25 quantile to the 0.75 quantile), and the vertical whiskers depict the range. The horizontal dashed red line depicts the elevation of breeding and natal territories.

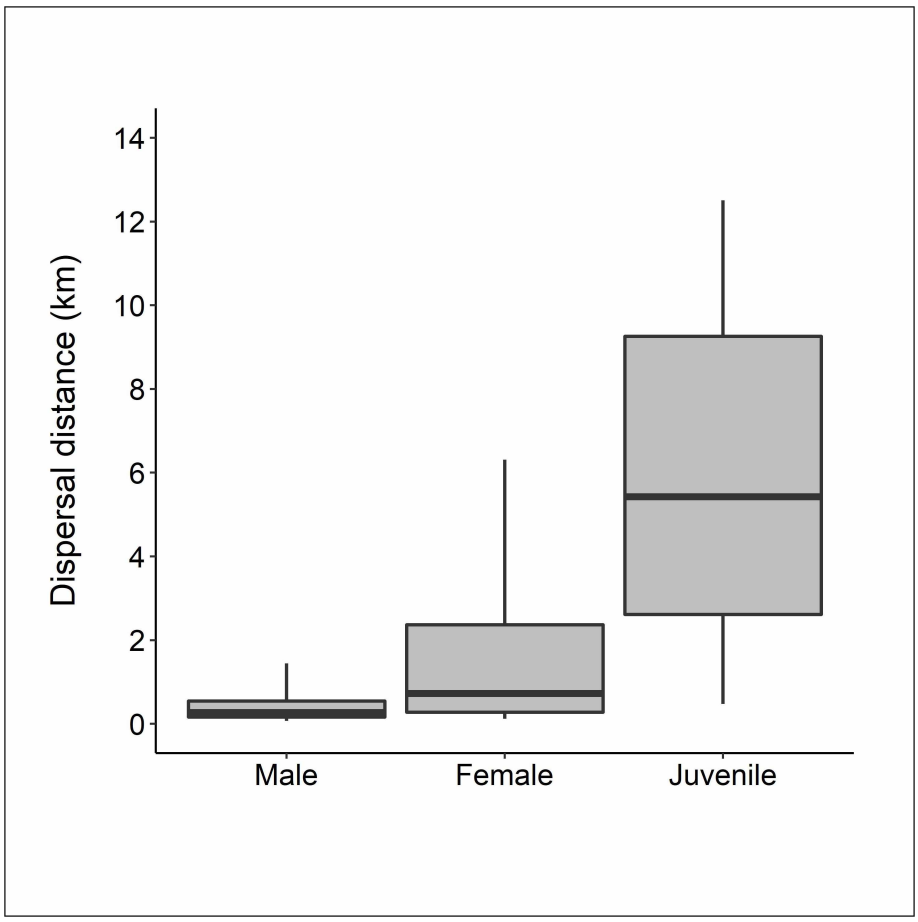

Figure 4.6: Distributions of breeding and natal dispersal distances for adult male, adult female, and juvenile willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA. The center horizontal lines depict median dispersal distances for each group, the gray box represents the interquartile range (the 0.25 quartile to the 0.75 quartile), and the vertical whiskers depict the range.

Chapter 5: Implications of Imperfect and Heterogeneous Detection for Landbird Monitoring: A Case Study with Ptarmigan[4]

5.1 Abstract

A fundamental component of wildlife population monitoring is the ability to obtain reliable estimates of population states (e.g., abundance, distribution) and vital rates (e.g., mortality, recruitment). An unavoidable complication shared by most monitoring techniques is an imperfect detection process, which has the potential to yield inaccurate estimates and inferences. We examined sources of variation in the detection process for willow ptarmigan (*Lagopus lagopus*), an ecologically and culturally valuable species. A variety of survey techniques have been used to estimate and index ptarmigan abundance, but the accuracy of the data produced by many of these techniques is unknown. We used temporally and spatially replicated counts and double observer sampling to model the detection process for point counts with acoustical broadcasts of territorial male ptarmigan vocalizations. We fit a generalized multinomial N-mixture model to estimate the availability of ptarmigan for detection as a function of time of season and time of day. We also estimated observer specific detection probabilities conditional on availability. Our results indicated negative effects of both temporal covariates on availability and substantial variation in observer specific detection probabilities (0.84 [95% CI: 0.77–0.89] – 0.98 [95% CI: 0.94–0.99]). These results suggest that using raw counts from ptarmigan point count surveys is a biased approach to estimation. Similarly, simulations suggested that using count indices to infer trends may be misleading, given the temporal variation in availability for detection and inter-observer variation in detection probability. We recommend that ptarmigan monitoring efforts account for imperfect detection and heterogeneity in the detection process prior to drawing inferences or making management decisions.

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5.2 Introduction

Wildlife population monitoring is an important component of managing ecological systems in the presence of human disturbance. This is particularly true for exploited populations (e.g., via hunting, fishing, trapping) that are managed for sustained yield. Information on population states and vital rates is necessary for understanding the impact of exploitation on the abundance and distribution of such populations, as well as for designing harvest strategies that seek to simultaneously maximize harvest opportunity, while ensuring population persistence. A ubiquitous problem in wildlife monitoring is imperfect detection of individuals during survey efforts (e.g., Ramsey and Scott 1979, Burnham et al. 1980, Nichols et al. 2009, Schmidt et al. 2013). Attempting to estimate abundance without accounting for imperfect detection yields bias in abundance estimators. A common approach to handling this bias is to treat estimates as indices of abundance, and to use those indices, rather than estimated abundance, to monitor temporal population trends. An implicit assumption in modelling trends with such data is that the rate of imperfect detection is constant over time (i.e., the same proportion of individuals remains undetected during all survey efforts throughout the duration of the monitoring). Although this assumption may be reasonable in some specific situations, many factors can result in heterogeneity in detection rates (Burnham 1981, Pollock et al. 2002, Nichols et al. 2009).

Further complicating this issue is variation in the sources of imperfect detection. The detection process can be decomposed into three general categories of detection error (Nichols et al. 2009): (1) presence, the probability that an individual is present in a sampling unit during a survey; (2) availability, the probability that an individual is available for detection given presence; and (3) detection, the probability that an individual is observed given presence and availability. Different survey methods account for different components of the detection process and it is important to recognize where detection error may occur in the context of specific sampling designs.

Ptarmigan (*Lagopus* spp.) are ecologically important species that are monitored in many

regions throughout their circumpolar ranges. They are key prey species for a variety of avian and mammalian carnivores and are thought to play an important role in the numerical cycles that are typical of many arctic and boreal vertebrates (Boutin et al. 1995). Moreover, they are culturally valued species for subsistence and recreational hunting in both North America and Eurasia. Hunting has been found to have varied effects on ptarmigan populations (e.g., Braun and Rogers 1971, Weeden 1972, McGowan 1975, Pedersen et al. 2004, Sandercock et al 2011). As such, rigorous monitoring strategies are needed for ptarmigan populations. A variety of survey techniques have been used to estimate and index ptarmigan abundance, but the accuracy of the data produced by many of these techniques is unknown. We examined the role of imperfect detection in willow ptarmigan (*Lagopus lagopus*) point count surveys with acoustical broadcasts in southern Interior Alaska, USA. Our objectives were to estimate: (1) diel variation in the availability of willow ptarmigan for detection, (2) intra-seasonal variation in the availability of willow ptarmigan for detection, and (3) observer-specific variation in the probability of detection of willow ptarmigan given availability. In addition, we used simulation to assess the implications of a heterogeneous detection process for monitoring trend based on ptarmigan count indices.

5.3 Study Area

We conducted this study in the southern Alaska Range and northern Talkeetna Mountains in southern Interior Alaska, USA (Figure ??). We carried out surveys along the Denali Highway, which is a gravel road connecting the Parks Highway at Cantwell, Alaska to the Richardson Highway at Paxon, Alaska. We focused survey effort between mile posts 19 and 55 (measured eastbound from Cantwell, Alaska) of the Denali Highway, which traverses contiguous occupied ptarmigan habitat. Human use of the road corridor is substantial and includes ptarmigan hunting, as well as non-hunting recreation (e.g., hiking, all-terrain vehicle use, snowmobile use). Elevations along the survey route are moderate, with a range of 850–1,230 m. The area is characterized by a mix of unvegetated rocky slopes, open tundra-

dominated hills, shrub tundra, and riparian areas. Shrub species are primarily dwarf birch (*Betula nana, B. glandulosa*), alder (*Alnus* spp.), and willow (*Salix* spp.). Lower elevations are characterized by subalpine spruce (*Picea* spp.) stands and taller stands of dwarf birch.

5.4 Methods

5.4.1 Field Methods

We conducted surveys for territorial male willow ptarmigan at pre-selected points, spaced systematically by 1.6 km, along the western Denali Highway. Two observers travelled between points in a highway vehicle between sunrise (ranging from 03:47 and 05:35 hrs) and 22:00 hrs. Upon arriving at a survey point, observers exited the vehicle and began the acoustical broadcast sequence, which entailed listening silently for 2 min, broadcasting recordings of male willow ptarmigan vocalizations for 2 min, and listening silently again for 2 min. Ptarmigan establish territories in the spring and are both conspicuous and responsive to recordings of conspecific vocalizations (Bergerud and Mercer 1966, Bergerud 1970, H$\acute{}$ornell and Willebrand 1997), with detections decreasing after approximately 5 minutes of surveying (H$\acute{}$ornell and Willebrand 1997). Each observer independently recorded the number of ptarmigan detected during the 6 min survey period. In addition, observers recorded: (1) the times at which survey periods began; (2) the times at which detections occurred; (3) the type of detection (aural, visual, both); (4) the distance and bearing at which ptarmigan were detected using a laser rangefinder and compass, respectively; and (5) observer identity. After each survey period was complete, observers compared their records and determined which individual ptarmigan had been detected by one observer, the other observer, and both observers. We conducted surveys between 1 May and 30 June during 2014 and 2015. We visited a total of 33 survey points during each of 5 occasions during each year.

5.4.2 Data Analysis

We used a Bayesian implementation of the generalized multinomial N-mixture model of Chandler et al. (2011) to model temporal effects on availability and observer-specific detection probability. We did not attempt to separately estimate the probability of being present in the sampling unit during the survey (i.e., 1-probability of temporary emigration) and the probability of being available for detection given presence in the survey unit. Therefore, our estimates of availability also pertain to the temporary emigration process and represent the probability of being present in the sampling unit and available for detection (i.e., either visible or audible). We specified the model as

$$M_i \backsim \text{Poisson}(\lambda)$$

$$\log(\lambda) = \alpha_0 + \alpha_1 \text{Elevation}$$

$$N_{it} \backsim \text{Binomial}(M_i, \phi)$$

$$\text{logit}(\phi) = \beta_0 + \beta_1 \text{Time} + \beta_2 \text{Time}^2 + \beta_3 \text{Date}$$

$$\boldsymbol{y}_{it} \backsim \text{Multinomial}(N_{it}, \boldsymbol{\pi}_{it})$$

$$\boldsymbol{\pi} = \{p^2, (1-p)p, p(1-p)\}$$

$$\text{logit}(p) = \gamma_0 + \gamma_1 \text{ObserverB} + \gamma_2 \text{ObserverC} + \gamma_3 \text{ObserverD}$$

where M_i is the superpopulation (i.e., the number of territorial males with territories overlapping the sampling unit) at site i with mean λ, $N_{i,t}$ is the available population at site i during occasion t, ϕ is the probability that an individual at site i is in the sampling unit during occasion t, $\pi_{i,t}$ is a vector of multinomial cell probabilities reflecting the double-observer

sampling design, and $y_{i,t}$ is a vector of double observer counts. We used elevation as a site-specific proxy for willow ptarmigan habitat, with associated parameter α_1 and intercept parameter α_0. Willow ptarmigan remain within a well-defined elevational band in the study area (95% of locations between 764–1277 m), and breeding densities vary in association with elevation (Chapter 3). We used time and date as temporal covariates on ϕ, which represented diel and intra-seasonal variation in availability, respectively. Observers A, B, C, and D were categorical covariates on p and represented the identities of the four observers who participated in the study. The parameters γ_1, γ_2, and γ_3 were estimated relative to the intercept, γ_0. We stacked data from the two years of surveys, which resulted in sampling units being defined as site-years, rather than simply sites.

We implemented the model in JAGS version 4.3.0 (Plummer 2017) using the front-end package jagsUI (Kellner 2016) in the R software environment (R Core Team 2017) and assessed convergence graphically using trace plots and with R-hat statistics (Gelman and Rubin 1992).

Geographic and demographic closure during the survey season were two key assumptions implicit in our analysis. Geographic closure is satisfied if ptarmigan in the superpopulation at each site maintain home ranges overlapping the site throughout the survey season. Demographic closure is satisfied if births, deaths, and immigration do not change the composition of individuals in the superpopulation at each site. The former is satisfied for willow ptarmigan in our study because they maintain exclusive territories throughout the survey season. The latter is likely violated to a small degree because of mortality events, but births do not affect the population of adult males (to which our inferences apply) and immigration occurs after to the survey season. A concurrent study in the same study area concluded that survival rates were relatively high during the survey season, especially for males (Chapter 2). Nevertheless, mortality may have had a small effect on estimates of seasonal variation in availability.

After fitting the model, we simulated annual counts using estimated availability and

observer-specific detection rates to assess the likelihood of detecting abundance trends using unadjusted point count data (i.e., indices). First, we generated hypothetical ptarmigan abundances, M_i, at each of $i = 50$ sites along a systematic elevation gradient corresponding to the range of elevations in our surveys (760–975 m). We generated these values from a Poisson distribution with λ equal to the estimated linear predictor for the state process in our empirical model. Next, we randomly sampled from a range of dates (01 May–30 May) and times (sunrise to 8 hours after sunrise, which is approximately noon, but varies slightly with date) during which ptarmigan surveys might reasonably occur, and we used the estimated linear predictor for availability to generate values for the binomial parameter, p. Availability rates for each of the i sites were generated from a binomial distribution with the N parameter equal to the hypothetical abundance at each site, M_i. We then randomly selected one of the four observers from our study to conduct the hypothetical surveys at all 50 sites during that year, and we used the associated estimate of detection conditional on availability to generate the final hypothetical count for each site. The hypothetical counts were then summed to represent the count index value for the first year. Next, we adjusted the hypothetical total abundance by a fixed proportion of the first years abundance and repeated the sampling procedure from the first year. We repeated this hypothetical sampling for five consecutive years and then simulated 10,000 iterations of the five-year time series. The result was a hypothetically true trend in ptarmigan abundance over a five-year time series and 10,000 iterations of a simulated survey process for that time series, which depended on variation in the timing of surveys and observer identity. We fit a linear trend to each simulated survey time series and compared the slopes to the slope for the hypothetically true trend in abundance. The entire simulation procedure was carried out for two hypothetical scenarios: an annual increase in abundance of 15% per year, and an annual decrease of 15% per year.

5.5 Results

Both availability and observer-specific detection were imperfect. Availability for detection was associated with both temporal covariates (Table 5.1). A sharp decrease in availability for detection occurred throughout the morning hours ($\beta_{1(time)}$ = -0.58, 95% CrI = -0.91 – -0.29; $\beta_{2(time^2)}$ = 0.12, 95% CrI = -0.04 – 0.28; Figure ??). A more subtle, but consistent decrease in availability occurred as the breeding season progressed ($\beta_{3(date)}$ = -0.36, 95% CrI = -0.615 – -0.117; Figure ??). Individual observers exhibited substantial variation in detection probability conditional on availability (Table 5.1, Figure ??). As expected, elevation was positively associated with abundance (Table 5.1, Figure ??).

Simulated unadjusted counts underestimated trend magnitudes for both the increasing and decreasing abundance scenarios (Figure ??). For the decreasing scenario, 99.8% of the simulated trends had slopes of lesser magnitude than the hypothetical true slope (-12.4%). The median slope for the simulated counts was -2.5%, with 21.1% of slopes falling within 1% of 0 (i.e., stable) and 18% with positive slopes. For the increasing scenario, 99.1% of the simulated trends had slopes less than the hypothetical true slope (19.2%). The median slope for the simulated counts was 3.8%, with 12.2% of slopes falling within 1% of 0 (i.e., stable) and 20.0% with negative slopes.

5.6 Discussion

When not accounted for, imperfect and heterogeneous detection has the potential to skew results from wildlife surveys. The resulting flawed inferences can lead to inadequate conservation efforts or inappropriate management strategies, especially when managing exploited species. Our results suggest that imperfect detection of ptarmigan can substantially affect estimates of abundance. Moreover, even when counts are viewed as indices of ptarmigan abundance, the detection process appears to be sufficiently heterogeneous that trends are likely to be incorrectly estimated, with noteable uncertainty even in the direction of the trend (i.e., positive vs. negative trend, Figure ??). This is consistent with a growing body

of evidence suggesting that uncorrected abundance indices are often unreliable for monitoring wildlife populations (Preston 1979, Nichols 1992, Pollock et al. 2002, Anderson 2003, Mazerolle 2007).

Imperfect detection is nearly ubiquitous in ecology, but investigators seldom partition error estimates into different components of the detection process. Our estimates of ptarmigan availability and detection were both imperfect and non-constant. Both diel and phenological changes in behavior are typical of breeding birds (Gill 1994) and can result in temporally heterogeneous detection during surveys (Best 1981, Robbins 1981, Skirvin 1981, Rosenstock et al. 2002, Schmidt et al. 2013). By partitioning our estimates into availability and observer-specific detection, we were better able to identify and estimate the causes of this detection error. Specifically, temporal change in the availability of ptarmigan for detection (i.e., changes in how audible or visible individuals are) appears to be an important source of temporally varying detection error. To our knowledge, the implications of these behavioral dynamics for ptarmigan surveys have not been previously evaluated, but our results clearly indicate their influence on survey efficacy. Estimating observer-specific detection separately from availability indicated substantial variation in the ability of individual observers to detect ptarmigan given they are available to be detected. This is problematic for long-term efforts that may employ different observers among years.

Our estimates of availability include the probability that an individual is present within the sampling unit during the survey. Although we did not estimate this aspect of the detection process separately, we are not aware of any plausible reason that temporary emigration to portions of home ranges outside of sampling units would systematically increase during the survey season. Thus, our estimates of availability trends should reflect changes in the probability that willow ptarmigan are audible and visible as both time of day and time of season change, rather than changes in the probability of temporary emigration.

Although it was not the focus of our analysis, abundance increased in association with elevation, as we anticipated. Within the elevation range sampled, this gradient represents

a shift in habitat from scattered spruce stands interspersed with large dwarf birch and other shrubs at the lower elevations to treeless low-shrub tundra with some larger willows along riparian corridors at the upper elevations. Proceeding upward in elevation, beyond the elevations sampled, shrubs became sparser and abundance of willow ptarmigan would eventually have decreased.

Despite large hypothetical changes in abundance over the course of five years, most simulated counts did not detect meaningful trends in abundance, with a substantial number of simulated counts indicating trends in the wrong direction (18% of trends with positive slopes in the negative scenario, 20% of trends with negative slopes in the positive scenario). Fewer than 1% of simulated counts indicated trends that were equal to or greater than the magnitude of the true hypothetical slope in each scenario (Figure ??). Given that investigators observe only single realizations of survey processes, it is unreasonable to assume that trend inferences are accurate when heterogeneity as great as that observed in our study is present. A common approach to addressing issues of detection heterogeneity is standardization (Heyer 1994, Anderson 2001, Farnsworth et al. 2002, Pollock et al. 2002, Thompson 2002). Although standardization of survey dates and times can help to address temporal heterogeneity in the availability of birds for detection, variation in observer-specific detection rates may still be problematic if identical observers are unavailable in consecutive years or if observer ability changes among years. Moreover, phenological variation can result in a lack of consistent biological timing even when calendar dates are standardized (Wilson and Bart 1985) and even perfect calendar standardization is often logistically difficult in field studies (e.g., because of weather, personnel schedules, vehicle problems, etc.). Nevertheless, logistical tradeoffs between standardized indices and detection-corrected estimates should be considered on a case by case basis, as standardized indices may yield worthwhile information in some cases (Johnson 2008).

Although our study was designed to evaluate the role of availability and detection heterogeneity in ptarmigan point count surveys specifically, the same aspects of survey method-

ology (diel timing, seasonal timing, observer characteristics) that influenced the detection process in our study are almost certainly relevant to other survey techniques as well. In fact, these survey characteristics have been identified as influential in surveys for a variety of taxa (Robbins 1981, Skirvin 1981, Bridges and Dorcas 2000, Weir et al. 2005, Schmidt et al. 2013). Various index and estimation methods have been used in monitoring ptarmigan abundance, including transect counts (Pelletier and Krebs 1997), point counts (Marty and Mossoll-Torres 2012), distance sampling (Pedersen et al. 2012), and plot searches (Mossop 1988). All of these methods have the potential to be negatively affected by the sources of imperfect detection and heterogeneity in availability and detection that we identified as influential in this study. Therefore, to avoid inaccurate inferences about population states and vital rates, we recommend that investigators assume the presence of imperfect detection and heterogeneity in the detection process until the absence of these phenomena can be demonstrated.

5.7 Acknowledgments

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5.9 Figures

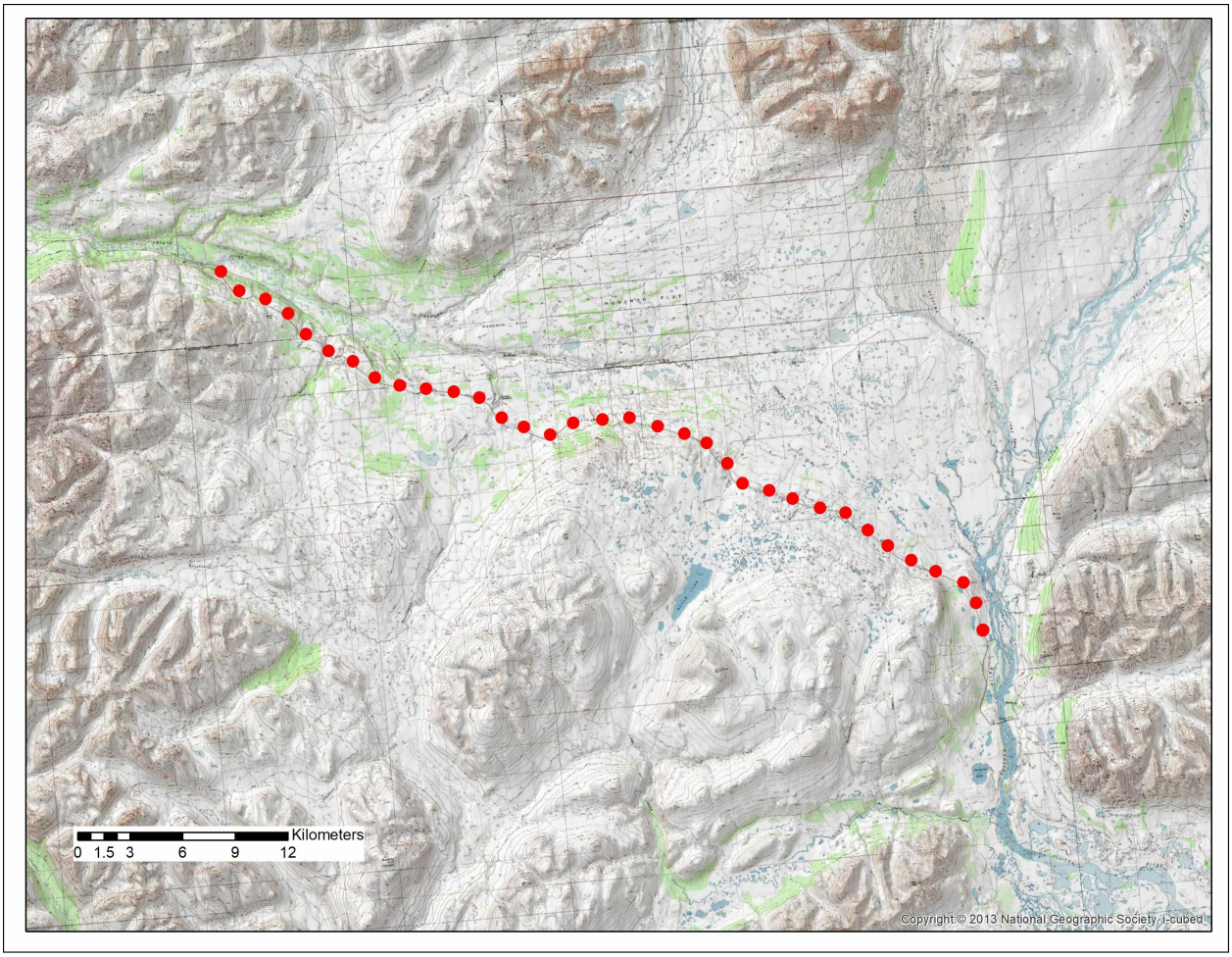

Figure 5.1: Sites of willow ptarmigan (*Lagopus lagopus*) surveys during 2014 and 2015 along the Denali Highway in southern Interior Alaska, USA.

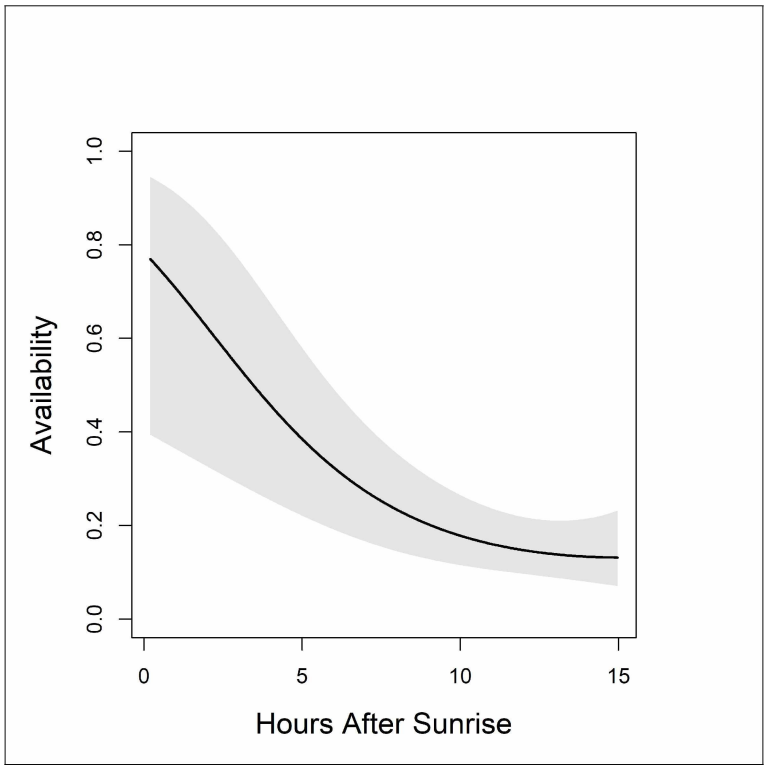

Figure 5.2: Probability of willow ptarmigan (*Lagopus lagopus*) being available for detection (i.e., audible or visible) during point count surveys in southern Interior Alaska during 2014 and 2015. The black line depicts the predicted values of availability as a function of time of day on 1 May and gray shading depicts the associated 95% confidence intervals.

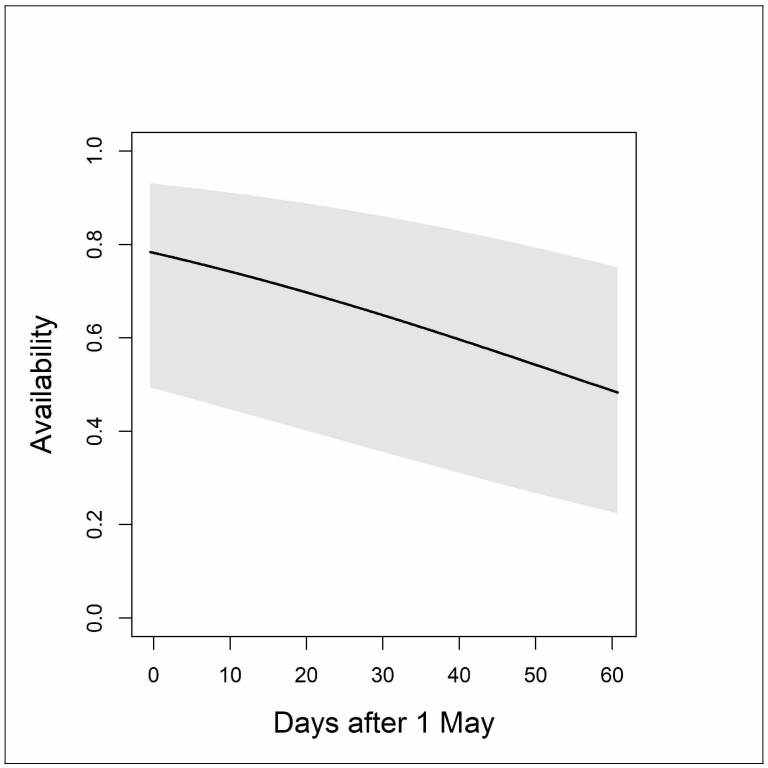

Figure 5.3: Probability of willow ptarmigan (*Lagopus lagopus*) being available for detection (i.e., audible or visible) during point count surveys in southern Interior Alaska during 2014 and 2015. The black line depicts the predicted being available for detection (i.e., audible or visible) during point count surveys in southern Interior Alaska during 2014 and 2015. The black line depicts the predicted values of availability as a function of date at two hrs after sunrise and gray shading depicts the associated 95% confidence intervals.

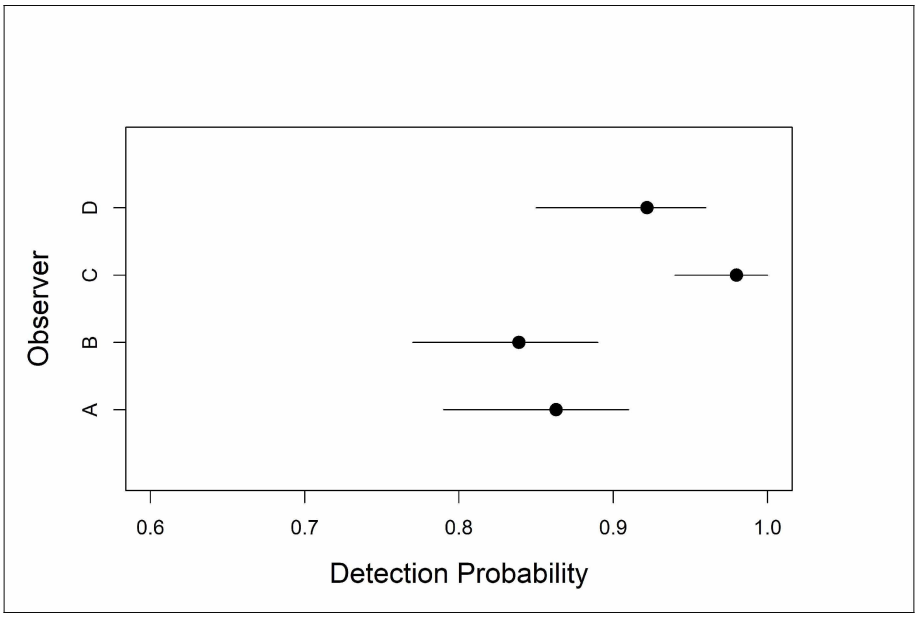

Figure 5.4: Probability of observer-specific detection of willow ptarmigan (*Lagopus lagopus*) conditional on availability during point count surveys in southern Interior Alaska, USA during 2014 and 2015. Black dots are point estimates for detection and lines represent the associated 95% confidence intervals.

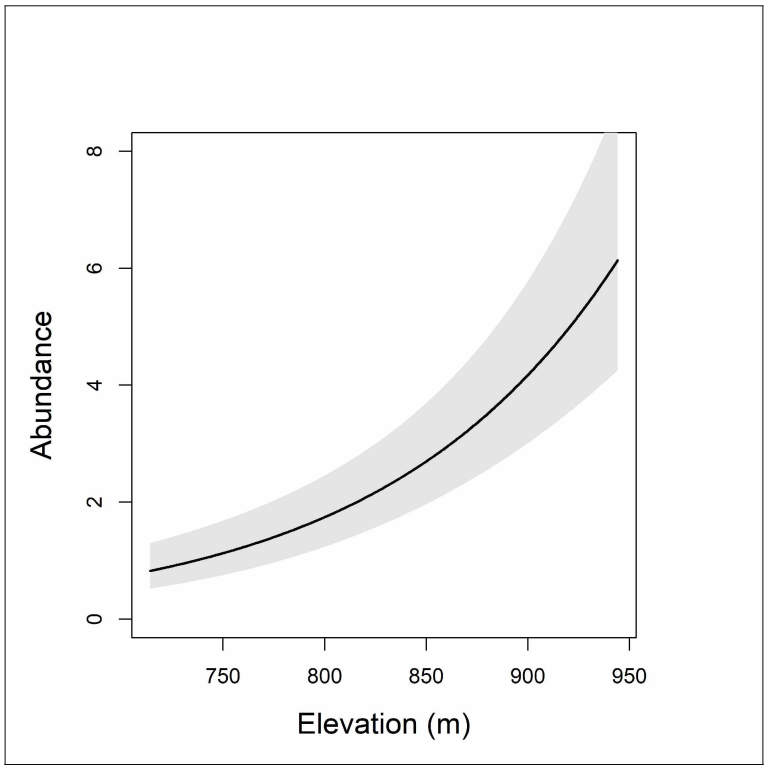

Figure 5.5: Estimated abundance of willow ptarmigan (*Lagopus lagopus*) at point count sampling units in southern Interior Alaska during 2014 and 2015. The black line depicts the predicted values of abundance as a function of elevation, which is a proxy for habitat. Gray shading depicts the associated 95% confidence intervals.

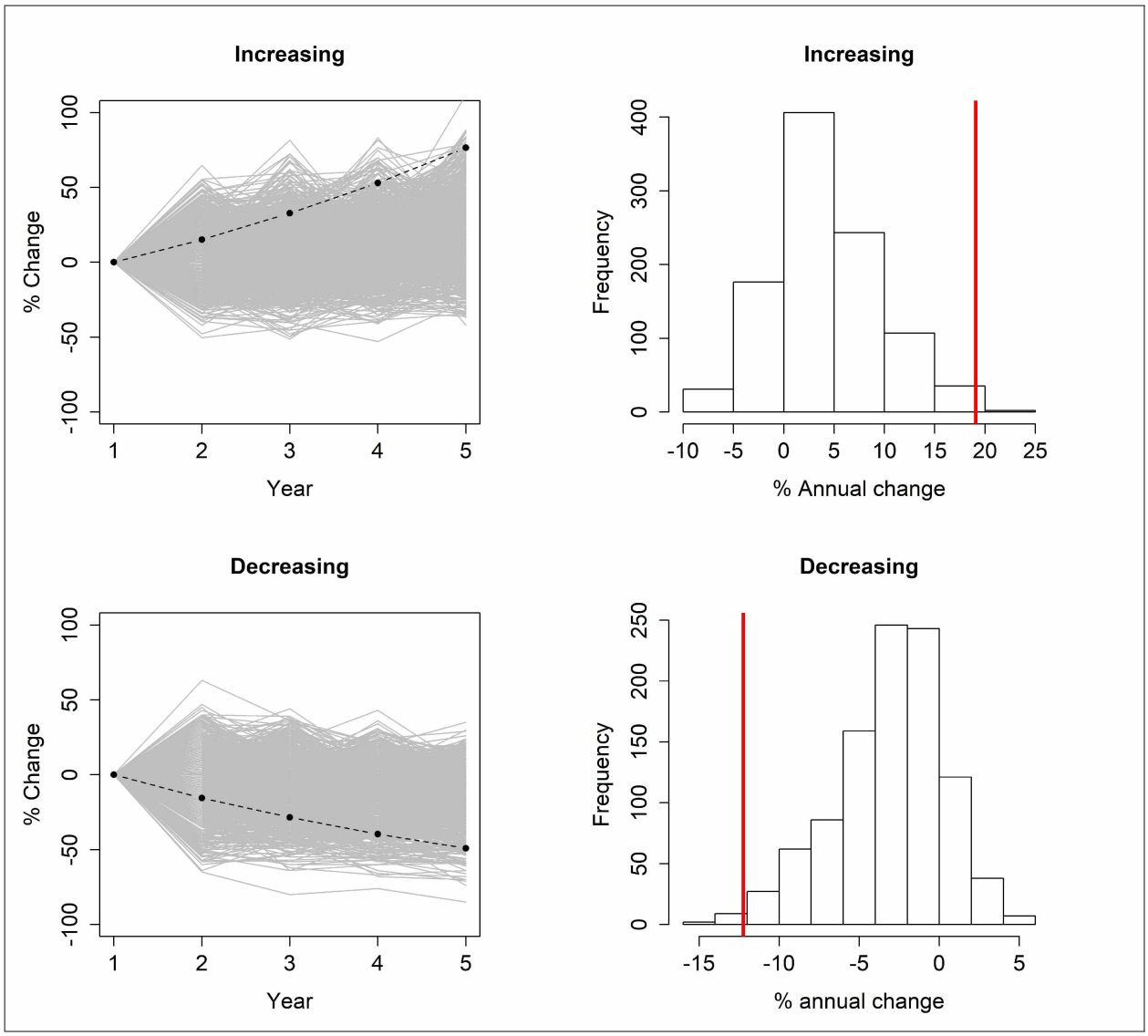

Figure 5.6: Hypothetical trends in abundance over a five-year time series and simulated point-count surveys used to evaluate the ability of count indices to detect trends in willow ptarmigan (*Lagopus lagopus*) abundance in southern Interior Alaska, USA. In the left panels, black dots and dashed lines depict the hypothetical trends in abundance (% change in abundance relative to the first year) and the gray lines depict realizations of simulated time-series counts. The right panels are histograms of slopes from fitting a linear trend to each simulated five-year count series and vertical red lines are the slopes of the hypothetically true trend.

5.10 Tables

Table 5.1: Parameter estimates for abundance, availability, and detection covariates from a generalized multinomial N-mixture model applied to willow ptarmigan (*Lagopus lagopus*) in southern Interior Alaska, USA.

Hierarchical level	Covariate	$\hat{\beta}$	Lower 95% CL	Upper 95% CL
Abundance	Intercept	0.846	0.440	1.529
(log scale)	Elevation	0.537	0.327	0.752
Availability	Intercept	-1.456	-2.262	-0.930
(logit scale)	Time	-0.581	-0.917	-0.286
	$Time^2$	0.119	-0.037	0.279
	Date	-0.357	-0.615	-0.117
Detection	Intercept	1.651	1.23	2.11
(logit scale)	Observer B	3.892	2.752	4.596
	Observer C	0.192	-0.536	0.992
	Observer D	0.813	-0.171	2.056

Chapter 6: General Conclusion

This dissertation enhances our understanding of willow ptarmigan population states and dynamics in relation to concentrated consumptive use by humans. In addition, this research has helped to elucidate aspects of general willow ptarmigan population ecology and survey methodology in subarctic Alaska.

In Chapter 2, I compared survival rates of willow ptarmigan in an access corridor heavily used by hunters to those from remote sites that receive little to no use by humans. Seasonal survival was lower at accessible sites than remote sites during the nesting, brood-rearing, and autumn dispersal seasons, but rates converged during the winter and pre-breeding seasons. This indicated a lack of seasonal compensatory mortality (Boyce et al. 1999, Kokko and Lindström 1998), and resulted in lower annual survival rates for ptarmigan at accessible sites. The seasons during which mortality was lower at accessible sites corresponded with the seasons in which ptarmigan were at or near their breeding/natal territories. Conversely, survival did not differ for birds from accessible and remote sites during seasons in which large seasonal movements resulted in a mixed spatial distribution of accessible and remote ptarmigan. This suggests that timing hunting seasons to correspond with seasonal movements away from breeding/natal territories may dampen the effect of harvest mortality on local breeders in access corridors. Conditional on our estimated vital rates, the disparity in annual survival between accessible and remote sites was sufficient to make breeding populations in the accessible areas unsustainable without net immigrationat least when populations are at a low phase in their fluctuations, as they were during this study (Schmidt et al. 2018).

Consistent with results from Chapter 2, I found that breeding densities in the accessible areas were substantially lower than those in the remote areas in Chapter 3. I used a spatially explicit distance sampling approach to estimate the density of willow ptarmigan breeding territories in the accessible and remote sites. As suggested by the projected growth rates based on vital rate estimates from Chapter 2, densities of ptarmigan breeding territories were

estimated to be low (1.8–3.7 territories per km^2) relative to those at remote sites (5.3–5.8 territories per km^2).

To better understand the role of movements in the vital rates and densities estimated in Chapters 2 and 3, I examined breeding/natal dispersal and seasonal movements of willow ptarmigan at our study sites in Chapter 4. Breeding dispersal distances were limited for both adult males (0.07–1.44 km) and adult females (0.12–6.31 km). Natal dispersal distances were longer and more varied (0.47–12.51 km). However, both breeding and natal dispersal distances were short enough to suggest that compensatory immigration is likely possible only when hunted areas are sufficiently small to allow dispersal from adjacent refugia. In contrast, observed seasonal movements were of sufficient magnitude to result in a spatially mixed distribution of birds from accessible and remote sites during the winter and early spring. This period of mixture temporally corresponded with all but the early ptarmigan hunting season, suggesting that these temporary seasonal movements may dampen the effect of harvest on accessible breeding populations both by reducing exposure of accessible breeders when they move into remote areas, and by increasing exposure of remote breeders when they move into accessible areas. The timing of movements away from breeding territories corresponded with the convergence of survival rates from Chapter 2, suggesting that seasonal movements may indeed aid in reducing the impact of harvest on accessible breeding populations.

In Chapter 5, I investigated the role of imperfect detection in willow ptarmigan point count surveys. Imperfect detection is a nearly ubiquitous issue in wildlife surveys but has only relatively recently garnered much attention (e.g., Ramsey and Scott 1979, Burnham et al. 1980, Nichols et al. 2009, Schmidt et al. 2013). I conducted point counts along the Denali Highway in southern Interior Alaska using acoustical broadcasts to elicit responses from territorial ptarmigan during the breeding season with a double-observer sampling design. I used a hierarchical model to partition imperfect detection into an availability component and an observer-specific detection error component. I included time-of-day and time-of-season as covariates in the availability model to estimate diel and seasonal variation in availabil-

ity of ptarmigan for detection. I found notable decreases in the availability of ptarmigan for detection as both time-of-day and time-of-season progressed. In addition, I estimated that individual observers varied substantially in their ability to detect available ptarmigan. Based on the estimated heterogeneity in availability and detection rates, I simulated a detection process over a five-year time series and assessed the likelihood of inferring trends correctly for both increasing and decreasing population scenarios. For both scenarios, the likelihood of correctly inferring the underlying trend was low, with greater than 99% of simulated detection processes underestimating the magnitudes of the trends. Our results suggest that investigators should carefully consider the potential problems with assuming constant and perfect detection in ptarmigan survey efforts to avoid drawing inaccurate inferences or making detrimental management decisions.

In summary, I found that survival rates and breeding densities of willow ptarmigan in heavily hunted areas were substantially lower than those in remote sites without hunting. I did not observe seasonal compensatory mortality and the potential for permanent immigration (i.e., breeding/natal dispersal) to compensate for harvest appeared limited. However, seasonal movements away from breeding territories appeared to distribute the effects of harvest more evenly among ptarmigan from accessible and remote areas during winter and early spring. This suggests that the timing of hunting seasons may play a critical role in determining impacts on ptarmigan densities in accessible breeding areas, with early season (prior to initiation of seasonal movements) harvest likely having the greatest impact. In addition, when examining ptarmigan survey methodology, I found substantial temporal heterogeneity in the availability of ptarmigan for detection during surveys, as well as variation in observer-specific detection rates. This underscores the importance of investigators considering the role of imperfect and heterogeneous detection when designing ptarmigan monitoring strategies to avoid inaccurate conclusions about abundance and trends.

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